

INTRODUCTION

The present study was suggested by the experiences of one of us (Reed) while sorting and identifying broken bones of numerous animals excavated from Neolithic sites in southwestern Asia. Identification of parts of skulls of small bovids, all presumably sheep and goats, was particularly difficult, a problem which led to our bisecting the skulls of wild and domestic sheep (*Ovis*) and goats (*Capra*) for detailed comparisons. The differences observed in cranial shapes and proportions suggested basic differences in the uses of horns and skulls, and thus of general behavior. Preliminary investigation of all genera of the bovid tribe Caprini (goats and sheep) showed the validity of the general assumption (Reed and Schaffer, 1966), and the present more detailed analysis of the correlated evolution of cephalic morphology and use of the horns and head followed.

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GENERAL CONSIDERATIONS

The tribe Caprini is composed of five genera: *Capra*, the goats and ibexes; *Hemitragus*, the tahr; *Ammotragus*, the arui, aoudad, or barbary sheep; *Pseudois*, the bharal or blue sheep; and *Ovis*, the true sheep (mouflons, argalis, and bighorn). Table 1 lists the taxa considered in this study of Caprini and related Rupicaprini along with common names and regions of occurrence. The plates include photographs of the intact skulls of representative species. The tribe Caprini is essentially Old World in its distribution and probably took its origin in Asia (Sushkin, 1925; McCann, 1956) from a group not unlike the so-called goat-antelopes (the rupicaprines *Nemorhaedus* and *Capricornis*) that live in this part of the world today. All of these animals are upland forms dwelling in mountainous areas, although some *Ovis* live on rolling hills and adjacent plains. As in other upland species, their fossil record is meager and their evolutionary history poorly understood (Simpson, 1945). Presumably, the sheep-goat line diverged from the true antelope during the middle Miocene (Pilgrim, 1939, 1947), but the details of this branching are left to conjecture. Antelopes whose horns are somewhat sheep-like have been found in the upper Miocene of Mongolia and in the European Pliocene (Pilgrim, 1934, 1939), but these are undoubtedly far from the main-line of Caprine evolution. Essentially modern sheep first appear in the upper Pliocene along with *Sivacapra*, a primitive relative of *Hemitragus* (Lydekker, 1898; Pilgrim, 1939, 1947). *Hemitragus*, *Capra*, and *Ovis* have all been found in Pleistocene deposits in Europe (Kurtén, 1968), and *Hemitragus* is also known from the Siwalik fauna of India (Colbert, 1935).

There are numerous features which distinguish the Caprini from their less specialized allies, the Rupicaprini (Reed and Schaffer, 1966). These characters include the following: 1. Increased size of the horns (both absolute and relative to the size of the skull); 2. Hypertrophy of the frontal bones and a concomitant relative reduction of the parietals (see fig. 9 for bones of skull); 3. Heightening of the skull as measured from the plane of the vertex to the foramen magnum; 4. Expansion of the frontal and cornual sinuses and the development of bony septa within these; 5. Bending of the basicra-

TABLE 1.—Populations of Caprini and Rupicaprini discussed in this paper.

CAPRINI			
Genus	Species	Common name	Geographical distribution
<i>Capra</i>	1a. <i>hircus aegagrus</i>	Pisang, Bezoar	Aegean Islands and mountains of southwestern Asia excluding Syria, the Levant, and all of Arabia except Oman
	1b. <i>hircus hircus</i>	Domestic goat	World-wide (introduced)
	2. <i>falconeri</i>	Markhor	Afghanistan and western Pakistan, and adjacent mountainous areas
	3a. <i>ibex caucasica</i>	Caucasian tur	Caucasus Mountains
	3b. <i>ibex sibirica</i>	Siberian ibex	Mountains of central Asia from Himalayas north into Siberia
	3c. <i>ibex nubiana</i>	Nubian ibex	Ethiopia, the Red Sea Hills of Sudan and Egypt, Sinai, and some parts of western Arabia
<i>Hemitragus</i>	1. <i>jayakari</i>	Arabian tahr	Oman (southeastern Arabia)
	2. <i>hylocrius</i>	Nilgiri tahr	Nilgiri Hills and adjacent ranges, southern India
	3. <i>jemlahicus</i>	Himalayan tahr	Himalaya Mts., from Kashmir to Sikkim; introduced, New Zealand
<i>Ammotragus</i>	1. <i>lervia</i>	Barbary Sheep, Arui, Aoudad	Hills and mountains of northern Africa, from Rio de Oro to Egypt and the Sudan
<i>Pseudois</i>	1. <i>nayaur</i>	Blue Sheep, Bharal	Mountains of central Asia, from Himalayas to Inner Mongolia
<i>Ovis</i>	1. <i>canadensis</i>	American Big-horn, Bighorn	Western North America, eastern Siberia
	2. <i>ammon</i>	Argali	Central Asia, from northern Himalayas to Mongolia and Siberia and west into Russian Turkestan
	3. <i>musimon</i>	Mouflon	Sardinia and Corsica; introduced in Europe
	4. <i>aries</i>	Domestic sheep	Introduced world-wide

TABLE 1.—Populations of Caprini and Rupicaprini discussed in this paper (Cont.)

RUPICAPRINI			
Genus	Species	Common name	Geographical distribution
<i>Rupicapra</i>	1. <i>rupicapra</i>	Chamois	European mountains from Spain to Caucasus and eastern Asia Minor
<i>Nemorhaedus</i>	1. <i>goral</i>	Goral	Southeastern Siberia, Manchuria, China, Korea, Tibet, Burma, Assam, Nepal, Punjab to Kashmir
<i>Capricornis</i>	1. <i>sumatrensis</i>	Serow	Kansu and southern China, and west to Burma, Nepal and Punjab; south into Indo-China, Malaya, Sumatra
<i>Oreamnos</i>	1. <i>americanus</i>	Rocky Mountain Goat	Northwestern North America

For a full survey of the species and subspecies belonging to the Caprini and Rupicaprini see Ellerman and Morrison-Scott, 1951.

nium in the region of basioccipital-basisphenoid fusion with the resulting ventrad rotation of the posterior elements of the braincase (fig. 11). In the acquisition of these characters, *Capra* has lagged, whereas *Ammotragus*, *Pseudois*, *Hemitragus jemlahicus*, and larger sheep display them to the extreme.

Since this study is to a large extent concerned with the complex of cranial characters associated with the horns, it is helpful to consider these structures in a general sense before proceeding to the individual genera and species. The bovid horn originates from the frontal bone and consists of a bony core surmounted by a corneous sheath. The horn core may or may not contain an air-filled sinus, but among the Caprini and their allies well-delineated sinuses exist in both frontal bones and horn cores. The sinuses of each side connect with each other and ultimately with the nasal passage and hence with the outside air. The basic pattern is illustrated in Figure 1. The figure shows a typical Rupicaprine, *Oreamnos americanus*, in which the outer table of the frontal bones has been removed. The skull of a Nubian ibex, *Capra ibex nubiana* was prepared in a similar fashion (fig. 2). From the figures, it is apparent that each frontal bone contains its own system of air cavities which are separated from those of the other frontal by a mid-sagittal septum. Each frontal bone is thus divided into dorsal and ventral tables, separated by the interpolation of the sinuses. Medially, the two tables are connected by the mid-sagittal septum; laterally, they come together to form the dorsal rim of the orbit. Sections of the skull in the sagittal plane

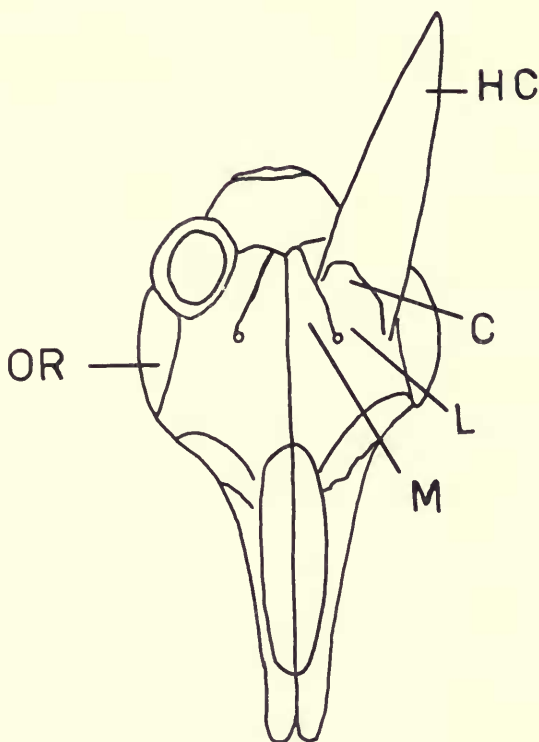


FIG. 1. *Oreamnos americanus* (Rupicapriini). The dorsal layer of the frontal bone and the frontal surface of the right horn core have been removed. The left horn core has been removed entirely. C—cornual sinus; HC—horn core; L—lateral branch of the frontal sinus; M—medial branch of the frontal sinus; OR—orbit.

(fig. 3) reveal the extent of the sinuses and the separation of the parts of the frontal bone. Each frontal sinus (left and right) is further subdivided into lateral and medial compartments by a septum that extends from the supraorbital canal posteriad. Anterior to the canal, the two compartments are united and the single sinus extends to the anterior edge of the frontal bone. The sinus of the horn core connects with the lateral compartment of the frontal sinus. In Rupicapriini, the sinuses are small and uncomplicated by the presence of additional internal septa; the cornual sinus is confined to the base of the horn core (fig. 1). In Capriini, the sinuses are relatively more extensive, and in many species there are numerous septa, mostly dorso-ventral, which have complex inter-relationships (see photographs, especially IX, XXIV, and XXVII); in addition, the lateral compartments of the frontal sinuses extend mediad behind the

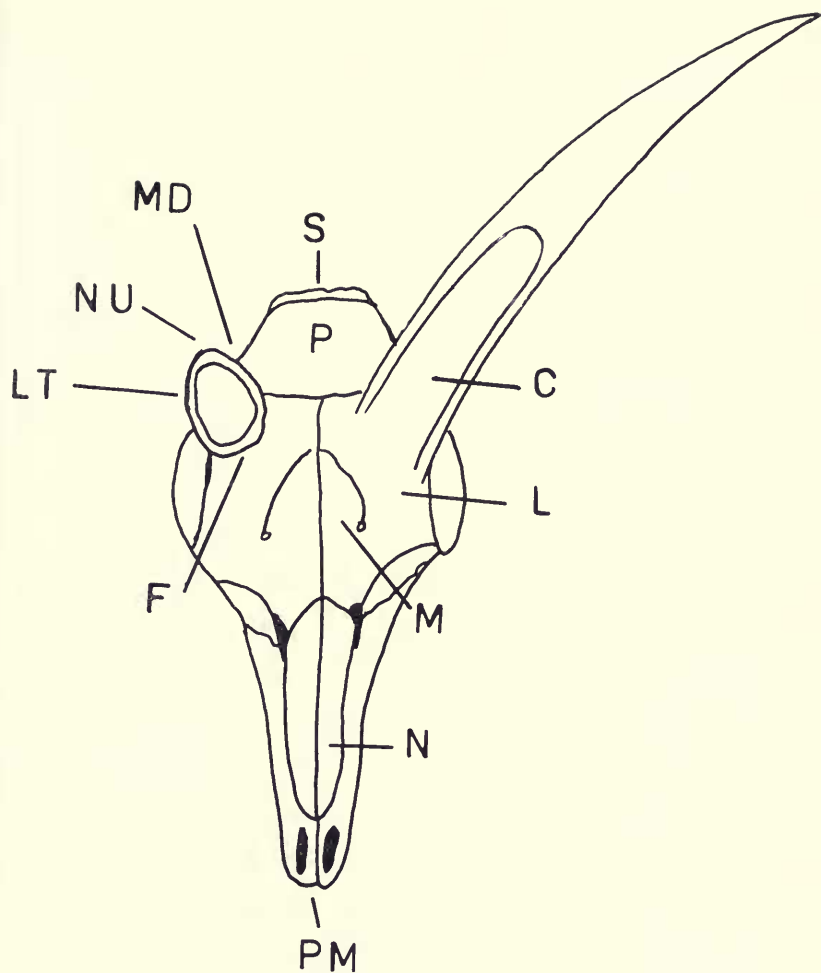


FIG. 2. *Capra ibex nubiana* (Caprini). Prepared in the same way as Figure 1. F—frontal surface of the horn core; LT—lateral surface of the horn core; MD—medial surface of the horn core; N—nasal bone; NU—nuchal surface of the horn core; P—parietal bones; PM—premaxillary bone; S—supraoccipital bone. Other letters as in Figure 1.

TABLE 2.—Measurements on skulls and horns of male and female *Nemorhaedus* and *Ammotragus*.

Measurement	<i>Nemorhaedus goral</i>						<i>Ammotragus leiria</i>					
	Males			Females			Males			Females		
	N	\bar{x}	s	N	\bar{x}	s	N	\bar{x}	s	N	\bar{x}	s
VL	7	14.5	.44	5	14.6	.26	5	21.7	.44	5	19.0	.67
FL	7	7.4	.33	5	7.4	.17	5	18.8	.88	5	13.5	.41
PL	7	3.5	.33	5	3.2	.25	5	2.1	.27	5	2.3	.36
CHC	4	6.6	.34	2	5.2	.56	5	25.8	1.3	5	14.9	.60
OLHC	4	7.9	.56	5	7.0	.88	5	43.5	5.6	5	25.4	1.3
OLHSh	7	14.3	1.5	5	13.7	1.4	4	61.0	8.1	4	36.0	2.1

KEY: N is the number of skulls measured; \bar{x} , the mean measurement in cm.; s, the standard deviation in cm.; and P, the level of significance given by the "t" test, comparing the measurements between the males and females. The reduced numbers of measurements on the horns resulted either from the authors' inability to remove horn sheaths, or from the fact that in two specimens of *Ammotragus* the sheaths were missing. See p. 14 for definitions of the measurements.

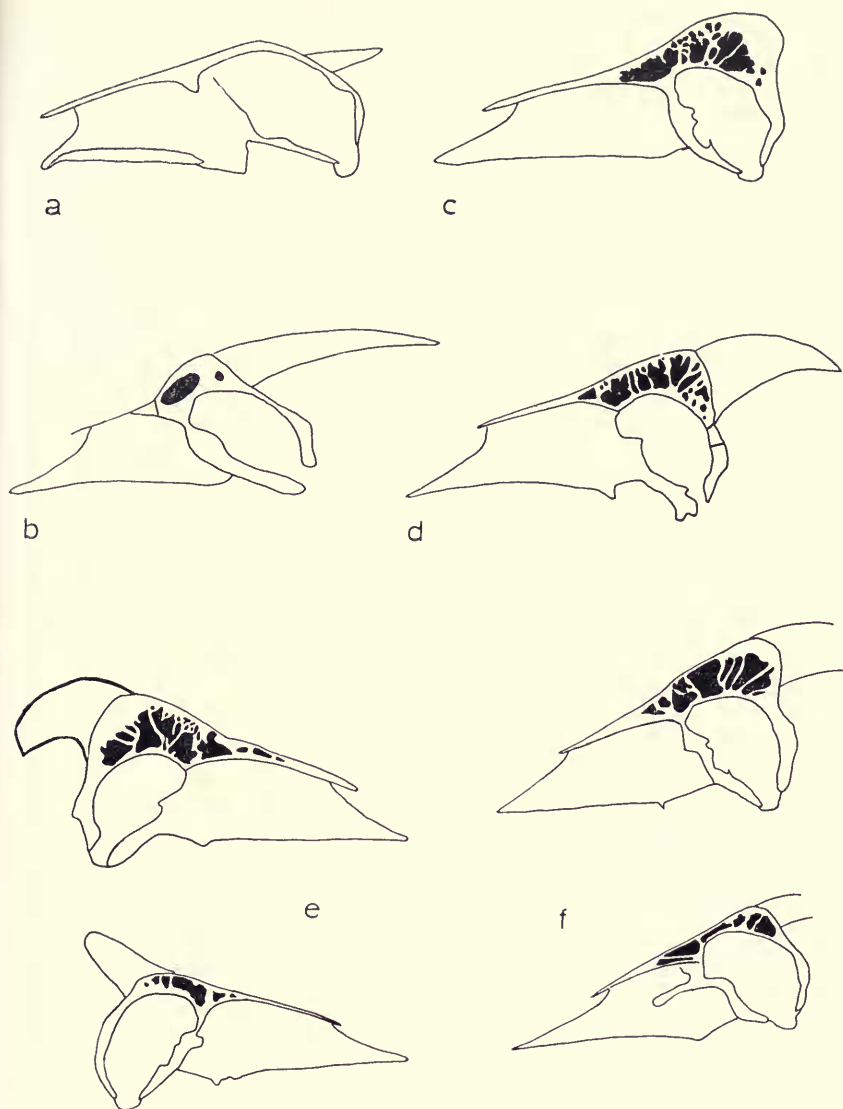


FIG. 3. Parasagittal sections (immediately to one side of the midsagittal septum) of several species. The sinuses are shown in black. a. *Nesotragus moschatus* (a primitive bovid without sinuses); b. ♂ *Capra hircus hircus*; c. ♂ *Pseudois nayaur*; d. ♂ *Hemitragus jemlahicus*; e. *Ovis canadensis*—top, male; bottom, female; f. *Ammotragus lervia*—top, male; bottom female.

medial compartments (fig. 2, *Capra*). This complexity is associated with an expansion of the bases of the horn cores. The cornual sinuses may also be more extensive and in some species extend to the very tips of the horn cores.

Sexual dimorphism with regard to the development of horns, sinuses, and associated structures is apparent in all Caprini and is considerably more pronounced than in rupicaprines. As an example, a series of male and female skulls of *Nemorhaedus goral* were compared for six cranial characters (table 2). Only two of the measurements revealed significant differences between the sexes ($P(t) > 0.95$). A similar comparison in a series of *Ammotragus lervia* revealed significant differences in five of the six measurements.

BEHAVIOR

All Caprini live in bands or herds and it would appear that this social situation has provided the basis upon which more complex behavioral relationships have been built. In all species studied, the males engage in some sort of intraspecific fighting, which typically involves combat with the horns. Such competition is an ancient trait in vertebrates, and is to be found in bony fish and a variety of tetrapods. Among the more specialized ruminants, the head, antlers, and horns have come to be used both as weapons and as parts of a stylized threat pattern (Geist, 1966b). Giraffes engage in contests in which long, swinging blows are delivered with the head (Innes, 1958); deer lock antlers and push and shove (Darling, 1937); musk-oxen charge and ram as sheep do (Teal, 1970); while the various antelope fight in a variety of ways (Walther, 1958, 1964; Estes, 1967). But whereas antelope fight primarily by locking horns and "wrestling" with their necks, the tendency to deliver sharp blows with the head and horns is characteristic of the Ovibovini, Rupicapriini, and the Caprini. Among Rupicapriini, the most vigorous form of combat appears to be body-butting, blows delivered with the horns to an opponent's flanks. Such behavior has been reported in *Oreamnos* (Geist, 1964), and *Rupicapra* (Couturier, 1938) and was undoubtedly antecedent to the more forceful head-to-head butting observed in male Caprini. Among the latter, although behavioral data are almost totally lacking for *Hemitragus* and *Pseudois*,¹ an interesting story unfolds.

The butting behavior of two young adult Caucasian turs (*Capra ibex caucasica*) was observed by one of us (Reed) at the Catskill Game Farm in New York. These males butted vigorously, horn to horn, and sometimes horn to forehead. Typically, one stood erect on his hind legs, took two or three steps forward, and then with neck down-arched crashed down upon his opponent. The male receiving

¹ Fragmentary descriptions of the fighting behavior of *Hemitragus hylocrius* (Hutton, 1947) and *Pseudois nayaur* (Lydekker, 1898) suggest that the former may engage in a type of butting behavior similar to that of *Ammotragus*, whereas the latter may ram more like true sheep.

the blow remained quadrupedal, moving his head to insure that contact was made properly, with horns crossed as typical for *Capra*. As in many such combats reported for other caprines, the whole thing appeared to be a cooperative affair which has led Reed to compare such "battles" with the joustings of medieval knights. In this instance, the male that initiated the contests was subdominant at the feed trough. Despite his seeming aggressiveness, he slowly withdrew up a precipitous slope. Walther (1961) has observed the same sort of behavior in other Caucasian turs and in the markhor, *C. falconeri*. He reports that in his experience both animals stand bipedally and stresses that the opponents are usually not oriented exactly head to head. As a result, the horns are crossed at the moment of impact. Similar observations have been reported for *C. ibex ibex* (Couturier, 1962), for *C. ibex sibirica* (in very anecdotal fashion by Grzimek, 1966), and for *C. hircus hircus* (Collias, 1956; Haefez and Scott, 1962; Scott, 1960).

In the case of *Ammotragus*, a different sort of fighting has been reported (Katz, 1949; Haas, 1959). Typically, the contestants approach each other quadrupedally with heads lowered in the customary threat posture. When they are almost together, they bring the heads down even further, thus directing the bases of the horns forward; this necessitates taking a few steps backward to make room for such a maneuver. Immediately after, they run toward each other and collide, the blow being delivered with the bases of the horns. Katz indicates that impact is horn to horn and that the heads are slightly tilted so that the horns are partly crossed. On the other hand, Haas reports that most of the blows are of the horn-to-forehead variety, so that the horns interdigitate. (Such interdigitation was observed by Reed about 10 per cent of the time in the Caucasian turs he observed.) No doubt both patterns occur. In addition, *Ammotragus* indulge in other forms of combat which include head-to-head pushing, horn hooking, and wrestling with the neck and horns.

Combative behavior in *Ovis* has been most thoroughly studied in the North American form *O. canadensis* in the Death Valley National Monument by Welles and Welles (1961). Their descriptions are mostly in agreement with other accounts (Murie, 1944; Geist, 1966a, 1969), but present more details. In the most spectacular form of combat, the opponents walk away from each other, whirl simultaneously, and rush toward each other at high speed. During the charge, which may cover as much as 30 ft., the animals run bipedally; the Welles estimate the closing velocity to range between 50 and 70 miles

per hour. Within the course of a few hours, a single pair may engage in several dozen such charges and rammings and show no signs of injury. Welles and Welles stress that the contesting males co-operate to insure exact horn-to-horn contact, although interdigitation (Geist, 1969) and other miscalculations are known to occur. Normally, a ram will not attack if his opponent is off balance or otherwise unprepared for battle. Indeed, the rare injuries that have been observed appear to result from the contestants having misjudged their approach. Walther (1961) has observed similar fighting behavior in *O. ammon poli*. Domestic rams charge at a lesser velocity and remain quadrupedal (Scott, 1960; Grubb, personal communication; Schaffer, personal observation).

The conclusion emerges from the foregoing discussion that the force of impact increases from *Capra* to *Ammotragus* to *Ovis* (Schaffer, 1968). Furthermore, as Geist (1966b) has indicated, strict "ramming" has been observed only in *Ammotragus* and *Ovis*. However, the heaviness of the bone and the complexity of the internal struts of the horn core (pl. XIX) and skull roof of *Pseudois nayaur*, coupled with observable damage to the horns of at least one specimen (pl. XVII), indicates to us that males of this population also use the horns in ramming, and in this aspect of their behavior are probably more like sheep than like goats. In the male of *Hemitragus*, the horn core (fig. 16c) and skull roof (fig. 3d) are also heavily braced internally, more so than in goats and ibexes, and we assume that the horns and skulls have evolved by natural selection, as in other Caprini, in correlation with the stresses to which the structures have been subjected. However, for the males of *Hemitragus*, no such head-to-head or horn-to-horn combats have been witnessed by Caughley (*personal communication*), who has observed for several years the Himalayan tahrs introduced into New Zealand. Even so, the fact that the total cranial structure of this particular species of tahr, *H. jemlahicus*, is of the configuration we have called "advanced" (p. 23), coupled with the other characters of horn cores and skull roofs mentioned above, leads us to believe that the males of *Hemitragus* also use their heads and horns in intraspecific combat, for the establishment of individual dominance, quite as other Caprini do. Only further study can substantiate or invalidate our assumption.

In contrast to the "ramming" of *Ovis*, and presumably of *Pseudois* and *Ammotragus*, the combats of *Capra* might better be described as "clashing," since there is no charge. Actually, in comparison to human activities, the male combats of the Caprini can best be com-

pared to jousting, in which opponents of nearly equal skill, weapons, and ability at defense compete in patterns of behavior common to both, and understood and expected by both. The contests are no less serious for all of that.

A final point, first observed by Geist (1968a) in bighorn sheep, concerns the age of first entry into the rut. Whereas both females and males are sexually mature by the end of the second year, males do not actually participate in rutting activity until their sixth, and often not until their eighth year. A shorter delay in the onset of reproductive activity has also been observed in *Hemitragus jemlahicus* imported into New Zealand (Caughley, personal communication). In this species, the males do not breed until the fourth or fifth year, although they become mature by the third year. Unfortunately, the Caprini have not been sufficiently studied to assert that this is a general characteristic of the group. Delayed male reproductive activity has been observed in other species in which dominance hierarchies exist among males (Sadlier, 1968), and we suspect that this situation is also true for most Caprini.

We should also point out that harem formation, as observed in pinnipeds and deer, is not a necessary prerequisite either for the development of delayed reproductive behavior or for the evolution of sexual dimorphism with regard to the structure of the horns, skull, etc. (see *Discussion*).

We shall, in the following sections, consider in greater detail the cranial anatomy of the Caprini and the relation it bears to the behavioral patterns just described.

Materials and Methods:

The following measurements were taken on the skulls and horns of more than 100 skulls of caprines and rupicaprines:

I. On the skull:

1. FL—*Length of the frontal bones*, as measured along the curve of the roof of the skull at the midline from the fronto-nasal suture to the fronto-parietal suture.
2. PL—*Length of the parietal bones*, as measured along the curve of the roof of the skull at the midline from the fronto-parietal suture to the parieto-occipital suture.
3. VL—*Ventral length of the skull*, as measured directly between the anterior edges of the maxillaries and the anterior edge of the foramen magnum.

II. On the horns:

1. CHC—*The basal circumference of the horn core.*
2. FN—*The fronto-nuchal (antero-posterior) diameter of the horn core,¹ measured at the base.*
3. LM—*The latero-medial diameter of the horn core,¹ measured at the base.*
4. OLHC—*The length of the horn core, along its frontal curve.*
5. OLHSh—*The length of the horn sheath, measured along the frontal surface.*
6. RAD—*The radius of the horn core, the radius of the hypothetical circle made by the first complete whorl of the horn, if the horn were to grow to that extent.*

In addition, permission was obtained from the American and Peabody Museums to section a total of 17 skulls. Sagittal sections of the horn cores and parasagittal sections of the skulls, barely to the right or left of the mid-sagittal septum, were prepared. On some specimens, the roof of the skull was also removed. Two angles were measured on the sectioned skulls (fig. 11) and the radius of the horn core (RAD) was determined, measured from the approximate center of the curvature to the midline of the sectioned horn cores.

¹ See Figure 1 for horn-surfaces.

COMPARATIVE CRANIAL ANATOMY

To facilitate consideration of the comparative cranial morphology, we have divided the material into three sections—horns, skull shape, and sinuses—to be followed by a discussion of the adaptive significances of some of the major features. Although no attempt has been made to provide detailed descriptions of the various species, we believe that we have indicated the main trends along with the obvious exceptions. The reader is again referred to the photographs of the intact skulls.

HORNS

Measurements are given in Table 3 for the horns of 11 species of Caprini and for *Nemorhaedus goral* and *Nesotragus moschatus*, the latter an extremely primitive antelope from East Africa.

In all Caprini, the horns of the males are longer and larger in cross-section than are those of females of the same species. Primatively, the horns were nearly straight, quite short, circular in cross-section and had their origin from the frontal bones slightly anterior to the posterior rim of the orbit. In addition, they did not rise above the facial plane. Thus, if a straight line were drawn along the top of the skull from the anterior edges of the nasal bones through the vertex of the skull and continued beyond, no part of the horn cores would lie above it. All of these characters are to be observed in the rupicaprine, *Nemorhaedus goral*. Among Caprini, however, most of these primitive characters have been modified. In general, the horn core is longer, more greatly curved along its main (proximo-distal) axis, elliptical—as opposed to circular—in cross-section, and in all but two species (*Hemitragus jemlahicus* and *Ammotragus lervia*), angled upward out of the facial plane. The radius of curvature is greatest in *Capra* (26–36.6 cm.), and this fact, and the extreme length of the horns and their upward angulation, is correlated with the displacement of the horn tips behind the skull. As in other Caprini, the horns (with rare exceptions) diverge from each other laterally, so that each describes a spiral in three dimensions (Thompson, 1945). In most caprines, only part of the first whorl is actually formed; this situation

TABLE 3.—Measurements on the horns of *Nesotragus*, *Rupicaprina*, and *Caprini*.

	N		CHC		OLHC		OLHSh		RAD	FN	LM
	M	F	M	F	M	F	M	F			
<i>Nesotragus moschatus</i> ¹	2	—	2.8	—	3.7	—	7.4	—	—	—	—
<i>Nemorhaedus goral</i>	7	5	6.6	5.1	7.9	7.0	14.3	13.4	—	2.1	2.1
<i>Capricornis sumatrensis</i>	8	4	10.1	9.2	13.6	11.4	22.5	18.7	—	3.0	3.0
<i>Oreamnos americanus</i>	7	3	12.7	9.1	10.0	8.1	22.7	22.2	—	4.2	3.9
<i>Rupicapra rupicapra</i>	5	—	7.2	—	9.0	—	22.0	—	—	2.4	2.1
<i>Capra hircus aegagrus</i>	3	3	15.3	6.8	46.2	12.4	73.8	20.4	28.5	5.1	3.6
<i>C. hircus hircus</i>	3	2	14.8	7.1	30.0	12.8	58.1	21.9	—	—	—
<i>C. ibex sibirica</i>	4	2	21.3	10.9	37.7	12.6	88.7	— ²	36.6	7.6	6.2
<i>C. ibex nubiana</i>	2	—	14.7	—	54.8	—	101.8	—	26.0	—	—
<i>Hemiragrus hylocrius</i>	2	2	16.3	11.4	18.6	13.0	34.1	26.5	—	5.4	3.8
<i>H. jemlahicus</i>	4	1	17.5	11.2	20.0	11.2	32.8	— ²	15.6	6.3	4.0
<i>Ammotragus lervia</i>	5	5	25.8	14.9	43.5	25.4	65.8	36.0	17.5	7.6	8.4
<i>Pseudois nayaur</i>	1	1	30.7	9.0	31.3	6.0	47.3	— ²	—	7.8	7.1
<i>Oris mustimont</i> ¹	2	—	16.2	—	22.8	—	56.9	—	13.0	6.0	4.5
<i>O. canadensis</i>	4	2	27.9	10.1	24.4	7.5	65+	17.5	16.0	9.9	7.9
<i>O. ammon</i>	4	3	32.9	12.4	43.1	13.0	105.6	42.1	13.9	11.6	9.3

KEY: All measurements in cm.; N—number; M—males; F—females

¹ Females hornless² Horn sheaths not available

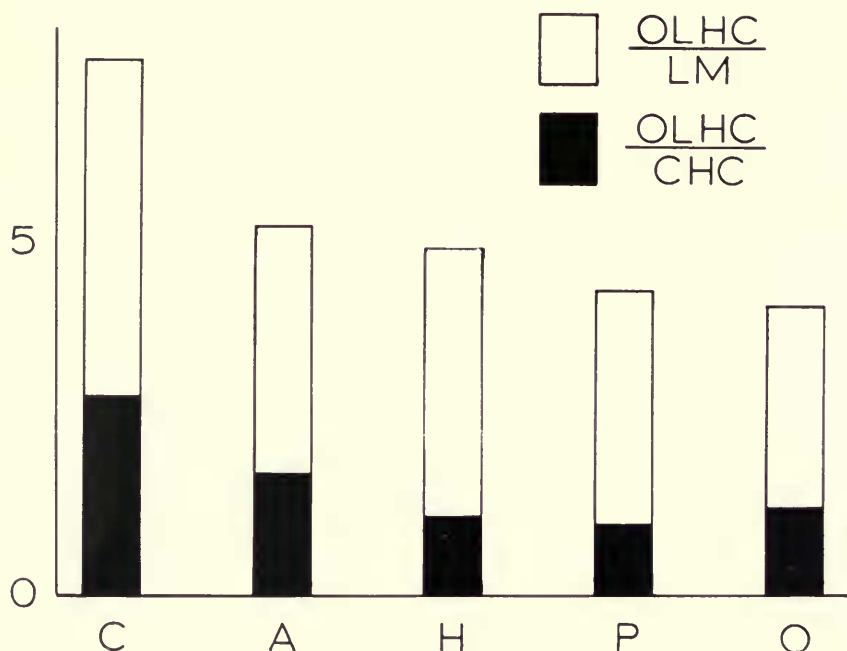


FIG. 4. Ratios of length of horn core (OLHC) to width of horn core (LM) and circumference of horn core (CHC) for the males of five genera of Caprini. C—*Capra*; A—*Ammotragus*; H—*Hemitragus*; P—*Pseudois*; O—*Ovis*.

results either from a low spiral angle (large radius), *Capra* and *Pseudois*; short horns, *Hemitragus*; or a combination of a moderately high spiral angle and moderately long horns, *Ammotragus*. Among species of the genus *Ovis*, however, long horns and high spiral angles produce the obviously coiled structure typical of the group. In some older rams, the horns may complete more than $1\frac{1}{2}$ turns.

In most Caprini, the horn bases are located above the posterior half of the orbit. In *Ammotragus lervia* and *Hemitragus jemlahicus*, however, the bases have been displaced behind the eye socket. The horn of *Pseudois* is unique in that the primitive frontal surface has been rotated mediad. As a result, the horns diverge from each other at an angle approaching 90° , and consequently only the tips extend behind the skull.

Relative to the basal circumference, the horns of *Capra* are longer than are those of the remaining genera (fig. 4); also, they are longer relative to the width of the frontal surface of the horn at its bases (latero-medial width). As a result, the horns of the various goats appear to be less "massive" than are those of other Caprini, even in

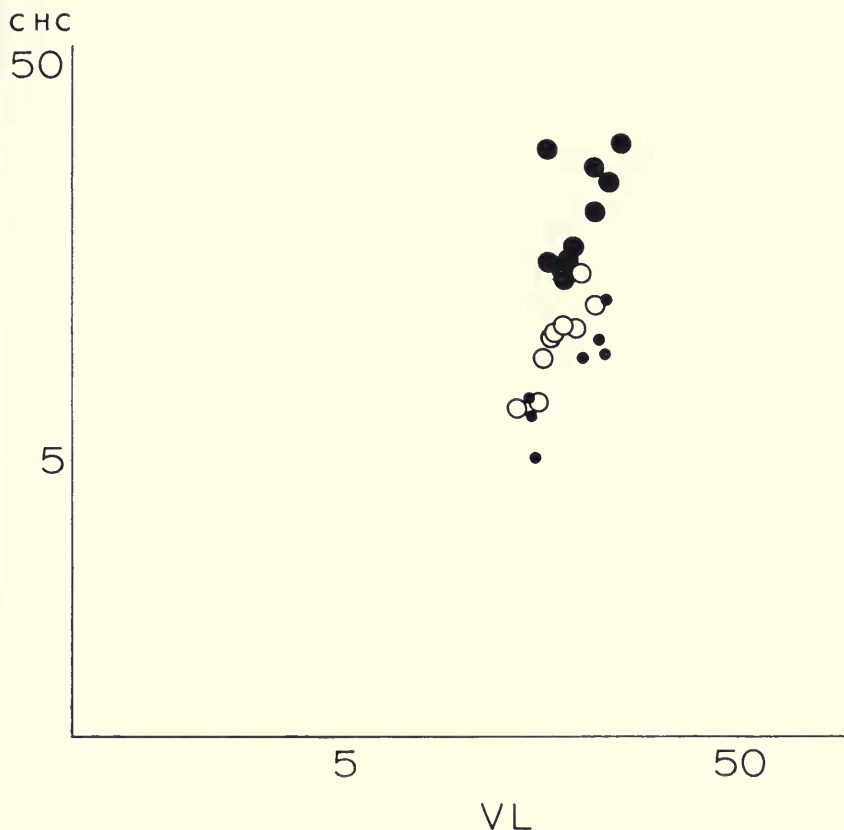


FIG. 5. Circumference of the horn core (CHC) plotted against length of skull (VL) for Rupicaprini (both sexes, small solid circles) and Caprini (large circles—solid, males; hollow, females). Log log plot. The slopes of the regression lines are: Rupicaprini, 1.3; female Caprini, 1.6; male Caprini, 2.0; see Table 7.

cases where they are absolutely heavier and larger in cross-section. In some populations (*C. hircus aegagrus*, *C. h. hircus*, and *C. falconeri*), the frontal surface has been further narrowed to form a median keel, but even in species with squared frontal surfaces (the ibexes), the frontal surface is not at all comparable in breadth (either absolutely or relative to the horn length) to that of the "sheep-like" Caprini—*Ammotragus*, *Pseudois*, and *Ovis*. The horns of *Hemitragus* present a special case; though extremely narrow, they are so short that the ratio of length of horn core to circumference approaches unity.

To a great extent (table 7), the size of the horns can be predicted from the ventral length of the skull. Figures 5–7 are log log scatter

OLHC

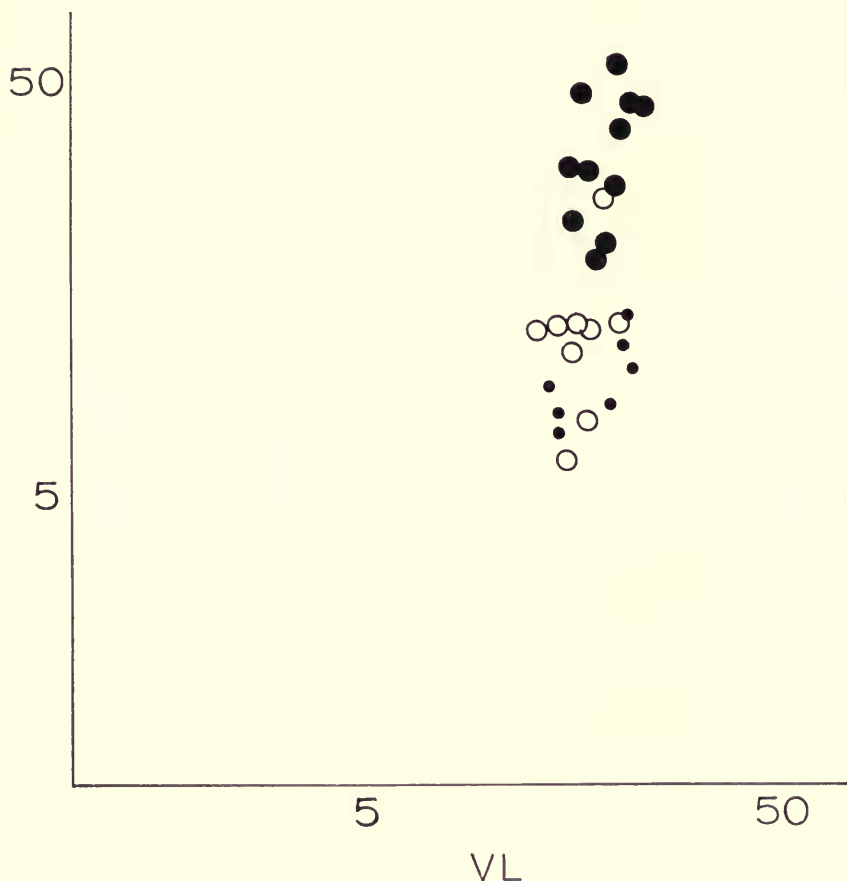


FIG. 6. Length horn core (OLHC) plotted against length of skull (VL) as in Figure 5. The slopes of the regression lines are: Rupicapriini, 0.8; female Caprini, 0.9; male Caprini, 1.4; see Table 7.

plots of the various horn measurements (CHC, OLHC, and OLHSh) against skull length (VL). Rupicaprines (male and female), female Caprini, and male Caprini are indicated by different symbols. The slopes of the regression lines are calculated in each case (table 7). In the case of each pair of measurements, the regression line was steepest for male Caprini, and least steep for the lumped Rupicapriini. Analysis by "t" test, however, indicates the differences in slope to be insignificant at the 0.05 level. Differences in the relative proportions of the horns and skull for the males of the different

genera and for the combined Rupicaprine males are shown in Figure 8. Relative to the length of the skull, *Ammotragus*, *Pseudois*, and *Ovis* have wider horns; *Hemitragus* has shorter horn cores and sheaths.

SHAPE OF THE SKULL

The following measurements for the skulls of 14 species of Caprini and Rupicaprini and for *Nesotragus moschatus*, are given in Table 4:

1. VL—Ventral length of the skull.
2. FL—Length of the frontal bones.
3. PL—Length of the parietal bones.

In addition, two angles were measured on skulls sectioned in the parasagittal plane (table 5). The angles are illustrated in Figure 11. Angle 1 gives the slope of the basioccipital bone relative to the plane of the palate; angle 2, the slope of the postero-dorsal wall of the skull.

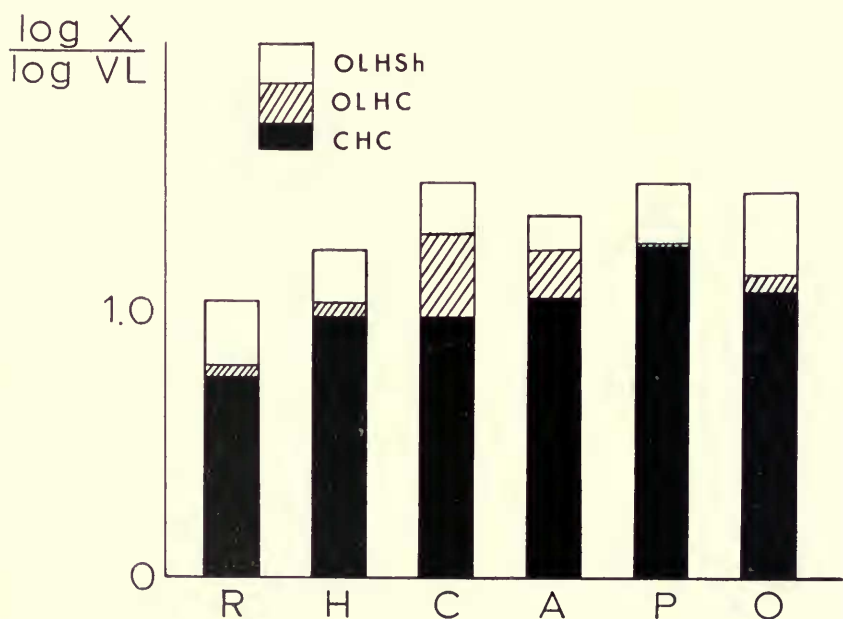


FIG. 8. Logarithms of horn measurements (X) divided by the logarithm of length of skull (VL) in male Caprini and Rupicaprini (R).

TABLE 4.—Measurements on skulls of *Nesotragus*, *Rupicapri*ni, and *Capri*ni.

	N		VL		FL		PL	
	M	F	M	F	M	F	M	F
<i>Nesotragus moschatus</i>	3	1	8.2	8.6	3.2	3.3	3.3	3.2
<i>Nemorhaedus goral</i>	7	5	14.5	14.6	7.4	7.4	3.5	3.2
<i>Capricornis sumatrensis</i>	8	4	21.3	21.0	11.0	10.1	5.1	5.5
<i>Oreamnos americanus</i>	7	3	22.0	19.5	9.0	8.2	4.4	4.0
<i>Rupicapra rupicapra</i>	5	—	14.1	—	8.0	—	3.9	—
<i>Capra hircus aegagrus</i>	4	3	16.9	13.1	10.0	7.4	4.0	3.1
<i>C. hircus hircus</i>	3	2	17.3	14.9	10.7	7.5	3.4	3.3
<i>C. ibex sibirica</i>	4	2	20.7	17.8	12.5	9.0	4.8	4.7
<i>Hemitragus hylocrius</i>	2	2	17.8	16.2	12.4	10.4	4.2	4.3
<i>H. jemlahicus</i>	4	1	18.3	16.0	15.8	12.8	2.3	3.0
<i>Ammotragus lervia</i>	5	5	21.7	19.0	18.8	13.5	2.1	2.3
<i>Pseudois nayaur</i>	3	2	15.9	15.4	21.2	9.0	2.3	3.0
<i>Ovis musimon</i>	2	2	15.8	13.5	10.8	8.2	3.3	2.8
<i>O. canadensis</i>	4	2	20.2	17.4	16.3	10.3	4.8	4.3
<i>O. ammon</i>	4	3	24.1	20.7	19.4	12.0	3.7	3.8

KEY: All measurements in cm.; N—number of specimens examined; M—males; F—females.

The positions and shapes of the various bones of the Caprine skull are presented in Figures 9, 10 (external), and 11 (internal).

Among Caprini, there are two basic cranial shapes. These we will designate primitive and advanced. As the names imply, the first configuration is similar to that observed in Rupicapri and other unspecialized Bovidae (fig. 3). Presumably, the ancestors of the sheep-goat line had skulls of this type. The characteristic feature is the fact that the postero-dorsal wall of the braincase projects behind the bases of the horn cores. Associated with this condition are the following characters: 1. Angle 2 is less than 50°, and 2. the parietal bones are at least 20 per cent as long as the ventral length of the skull (VL). Such a primitive configuration of the skull is observable in all species of *Capra*, in *Hemitragus jayakari* and *H. hylocrius*, and in *Ovis musimon*. The advanced skull is distinguished by the placement of the foramen magnum beneath the horn bases. As a result, the back of the skull becomes more nearly vertical. Angle 2 is greater than 70°, and the ratio of parietal length (PL) to ventral length of the skull (VL) is reduced to about 15 per cent. *Hemitragus jemlahicus*, *Ammotragus lervia*, *Pseudois nayaur*, and *Ovis ammon*

have skulls that may be classified as advanced, while *Ovis canadensis* is intermediate in skull shape between the two categories. Thus, of the five genera, one (*Capra*) has retained the ancestral pattern, two

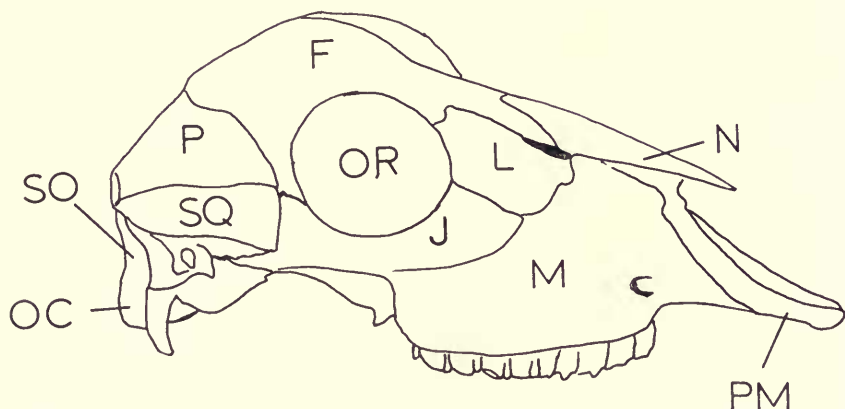


FIG. 9. Lateral view of skull of female *O. musimon*. F—frontal bone; J—jugal; L—lacrimal; M—maxilla; N—nasal; OC—occipital condyle; OR—orbit; P—parietal; PM—premaxilla; SO—supraoccipital; SQ—squamosal.

(*Ammotragus* and *Pseudois*) have evolved the advanced shape, and the remaining two (*Hemitragus* and *Ovis*) contain species with both configurations (fig. 3). Obviously, considerable independent and parallel evolution has occurred in several of the Caprine genera, but study of these factors will not be undertaken here. These comments on skull shape apply only to males. Among females the skull shape tends either to be primitive—in species with primitive males—or intermediate between the male configuration and the primitive pattern—in species with advanced males (fig. 3; table 5).

Although at least four species have advanced skulls, the means by which this configuration has been obtained differ. In *Ammotragus*, *Hemitragus jemlahicus*, and *Ovis canadensis* (to the extent that *O. canadensis* is advanced), the braincase has actually been rotated ventrad. This is best seen by observing the inclination of the basioccipital relative to the plane of the palate (angle 1). Among the primitive species, this angle is low (12° in *Ovis musimon*; 24° – 29° in the different species of *Capra*); in the species that have rotated braincases the angle is higher (36° – 41°). In *Pseudois* and *Ovis ammon*, on the other hand, the advanced configuration has been obtained by posterior growth of the frontal bones. Angle 1 has remained low (24° in *Pseudois*; 15° in *O. ammon*), while the length of the frontal

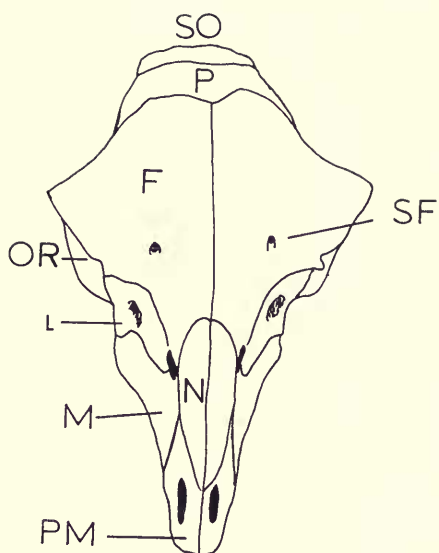


FIG. 10. Top view of skull of female *O. musimon*. SF—supraorbital foramen; other bones labelled as in Figure 9.

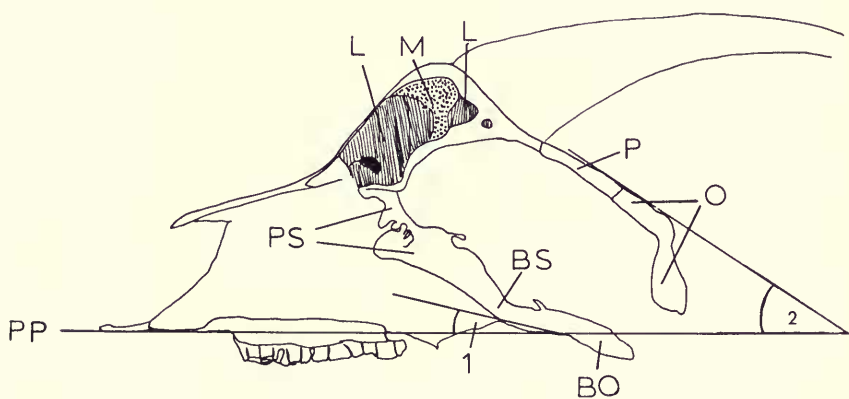


FIG. 11. Parasagittal section of *Capra hircus hircus* illustrating the bones of the basicranium and the angles measured. BO—basioccipital; BS—basisphenoid; L—lateral branch of the frontal sinus; M—medial branch of the frontal sinus; O—supraoccipital bone; P—parietal bone; PP—plane of the palate; PS—presphenoid; 1—angle 1; 2—angle 2. Both angles are taken relative to the plane of the palate.

TABLE 5.—Measurements of Angles 1 and 2, skulls of Caprini.

Species	Shape	Angle		FL	$\frac{FL}{PL}$	$\frac{PL}{VL}$
		1	2			
<i>Capra hircus aegagrus</i>	Primitive	24	27	10.0	2.5	.24
<i>C. hircus hircus</i>	Primitive	25	40	10.7	3.2	.20
<i>C. ibex sibirica</i>	Primitive	29	43	12.5	2.6	.24
<i>Ovis musimon</i>	Primitive	12	48	10.8	3.2	.21
<i>Hemitragus hylocrius</i>	Primitive	—	—	12.4	3.0	.24
<i>Ovis canadensis</i>	Intermed.; rot.	36	75	16.3	3.4	.24
<i>Hemitragus jemlahicus</i>	Advanced; rot.	40	74	15.8	7.0	.13
<i>Ammotragus lervia</i>	Advanced; rot.	41	84	18.8	9.0	.10
<i>Pseudois nayaur</i>	Advanced; back	24	92	21.2	9.2	.14
<i>Ovis ammon</i>	Advanced; back	15	78	19.4	5.2	.15
<i>Capra hircus hircus</i> (F)	Primitive	25	48	7.5	2.3	.22
<i>Ovis canadensis</i> (F)	Intermed.; rot.	36	72	10.3	2.4	.25
<i>Ammotragus lervia</i> (F)	Intermed.; rot.	13	56	13.5	5.9	.12

KEY: Angle measurements in degrees, FL in cm.; F connotes female; rot.—rotation of the braincase; back—backward growth of the frontal bones.

bones has increased greatly. In all species with advanced skulls, angle 2 is greater than in primitive species (74° – 92° vs. 27° – 48°); the frontal bones are absolutely longer; the ratio $\frac{FL}{PL}$ is greater; and the ratio $\frac{PL}{VL}$ is smaller. These considerations are summarized in Table 5.

In species with advanced skulls, little correlation exists between parietal length and skull length. Among species with primitive skulls such a correlation does exist (figs. 12, 13). Among all species, there is a fairly good correlation between frontal length and ventral length (fig. 14). Regression analysis yields slopes of 0.6 for Rupicaprini, 1.1 for females of Caprini, and 1.6 for males of Caprini excluding *Pseudois* (table 7; see *Discussion*). Ratios of $\frac{\log FL}{\log VL}$ for each genus and for the Rupicaprini lumped are given in Figure 15.

SINUSES

The fundamental plan of the caprine sinus system was discussed in the section on *General Considerations*. Figures 1 and 2 depict the sinuses as viewed from above the skull with the external tables of the frontal bones and frontal surface of the horn core removed; Figure 3 depicts the skulls of several species in para-sagittal section revealing the extent of the frontal sinus in each. Figure 16 presents horn cores sectioned in the sagittal plane. Additional examples of sectioned skulls and horn cores are reproduced in the photographs.

TABLE 6.—Data on skulls and cranial sinuses, Rupicaprini and Caprini.

Species	Skull		Frontal sinus				Cornual sinus			
			Extent		Septa		Extent		Septa	
	Sex	M	F	M	F	M	F	M	F	M
<i>Oreamnos americanus</i>	P	P	N	*	U	*	N	*	U	*
<i>Rupicapra rupicapra</i>	P	P	N	*	U	*	N	*	U	*
<i>Capra hircus aegagrus</i>	P	P	N	*	U	*	E	*	U	*
<i>C. hircus hircus</i>	P	P	N	N	†	U	†	†	†	U
<i>C. ibex sibirica</i>	P	P	N	*	†	*	†	*	U	*
<i>C. ibex nubiana</i>	P	P	*	*	*	*	†	*	U	*
<i>Ovis musimon</i>	P	P	†	*	†	*	†	†	†	†
<i>O. canadensis</i>	I	I	E	†	C	†	E	E	C	U
<i>O. ammon</i>	A	A	†	*	C	*	†	*	C	*
<i>Hemitragus jemlahicus</i>	A	I	E	*	C	*	E	*	U	*
<i>Ammotragus lervia</i>	A	I	E	†	C	†	E	E	C	†
<i>Pseudois nayaur</i>	A	I	E	*	C	*	†	*	C	

KEY: Skull—skull shape, see Table 5; Extent—extent of sinus;

*—specimens not available for section; +—females hornless;

P—primitive; A—advanced; I—intermediate;

N—not extensive; †—moderately extensive; E—extensive;

U—uncomplicated; ‡—moderately complex; C—complex.

The extent of the frontal sinuses is correlated with the shape of the skull. In species with advanced skulls, the sinuses overlies most, if not all, of the brain; in species with primitive skulls, the sinuses cover only the anterior third of the brain. Since the sinuses penetrate approximately to the posterior edge of the frontal bones in all species, the position of the fronto-parietal suture is the prime determinant of the proportion of brain overlaid by sinus.

Unlike the frontal sinuses, the cornual sinuses vary from species to species in what appears to be an unpredictable fashion (table 6). For example, in *Capra hircus aegagrus*, they extend to the very tips of the horn cores, while in the domestic goats (*G. h. hircus*) observed by us, they are confined to the horn core's basal third. A similar situation is to be found in the genus *Ovis*, where the cornual sinuses are extensive in *O. canadensis*, but relatively short in *O. musimon* and *O. ammon*.

Within the sinuses are the bony septa. Primitively, these are few in number and are almost totally absent in *Rupicapra* and *Oreamnos*. Each frontal sinus does, however, contain the strip of bone that divides the sinus into lateral and medial compartments (see figs. 1, 2). In species with primitive skulls, this septum may be the

only one in each frontal sinus. Other septa, if present, are few in number and irregularly placed; there is a tendency to form rings of bone that extend like hollow pillars between the ventral and dorsal tables of the frontal bones, but this is very slight. In species with advanced skulls, this tendency is more pronounced. Removal of the dorsal portion of the frontals reveals a pattern like a honey comb, which is most complex in *O. canadensis* and *Pseudois nayaur*, but is also apparent in *Ammotragus lervia*, *Hemitragus jemlahicus*, and *Ovis ammon*. Viewed in para-sagittal section, the septa appear to be dorso-ventral struts. The tendency to interlock and form columnar structures can be appreciated only by removal of the outer table of the frontal bones (see pls. XIV, XIX, XXV, XXVII, XXVIII, XXX, XXXI).

For each species, the complexity of the cornual septa usually parallels that of those within the frontal sinus. Thus, in many *Capra*, cornual septa are almost entirely lacking. Those that do exist are

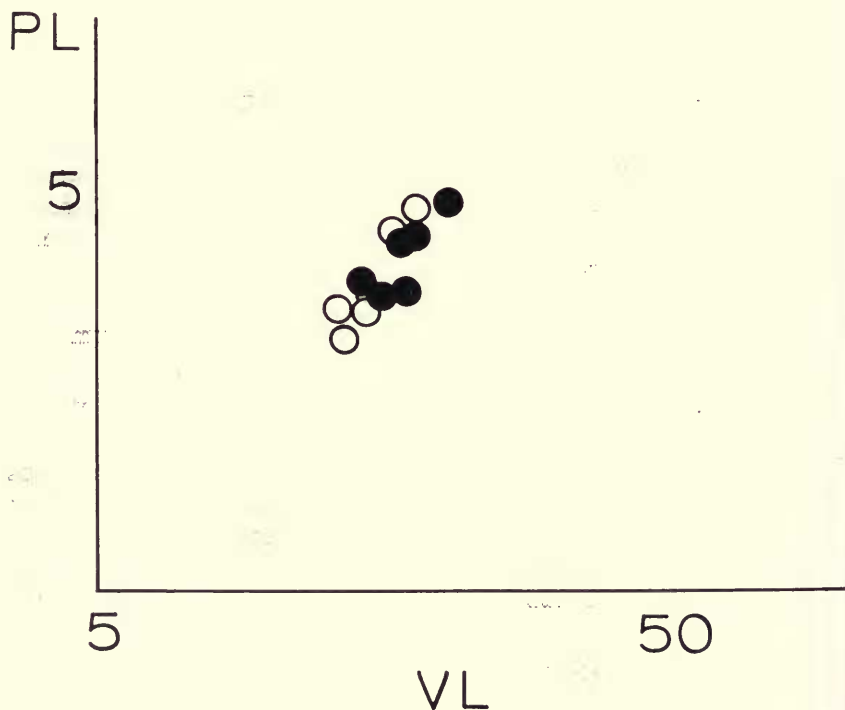


FIG. 12. Parietal length (PL) plotted against length of skull (VL) for Rupicaprini and primitive Caprini together. Log log plot; correlation coefficient $r=0.86$, $P>.999$. Solid circles males; hollow circles females.

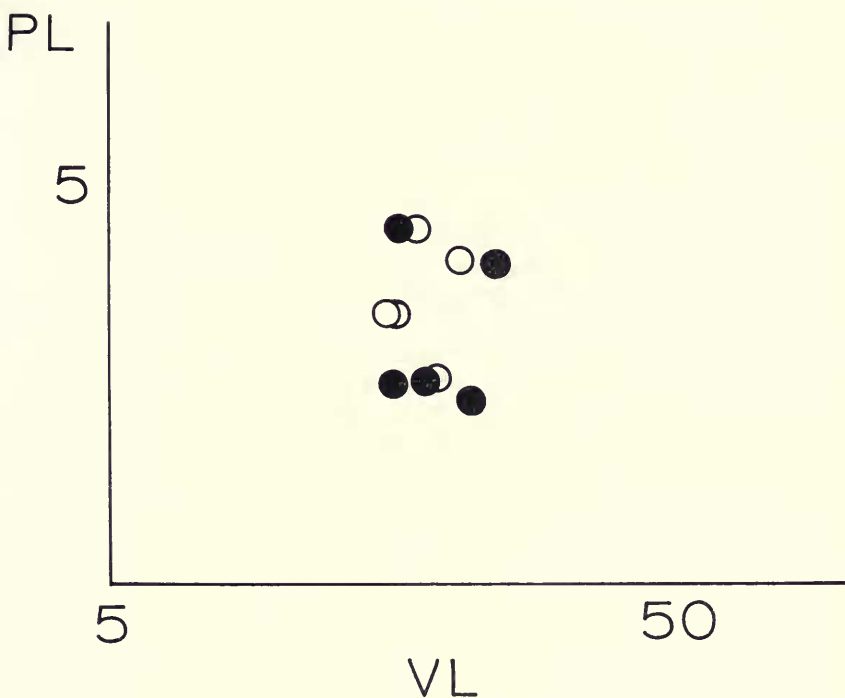


FIG. 13. Parietal length (PL) vs. length of skull (VL) for advanced Caprini, as in Figure 12. $r=0.18$; $P < 0.9$.

short processes originating from the interior side of the frontal surface and extending proximally toward the center of the core.¹ More complex patterns exist in other genera, and these seem to have been produced by the posterior extension of the septa into the horn base where at least some attach to the septum dividing the lateral and medial compartments of the frontal sinus. Primitively, the cornual septa appear to have been nearly flat structures originating from the inside of the frontal surface and joining the lateral and medial surfaces. In advanced Caprini the cornual septa form hollow tubes (figs. 16, 17). As with the septa in the frontal sinuses, this condition is best observed in *Ovis canadensis* and *Pseudois nayaur*. Even in these, however, the underlying pattern is unchanged as revealed in an adolescent *O. canadensis* (pl. XXIV). No matter what the

¹ In the alpine ibex (*Capra ibex ibex*), however, Couturier (1962) has observed intracornual septal structure of approximately the same complexity which we have observed in *Ovis musimon*.

degree of septal complexity, all cavities of the sinus system are confluent with each other and with the nasal passages.

In primitive species, the frontal sinuses of the females are similar to those of the males; in advanced species the frontal sinuses of the females are less extensive than those of the males. This sexual dimorphism agrees with differences in skull shape between the sexes and the correlation of the extent of the sinus with cranial shape. In all species, the septa within cornual and frontal sinuses of the females are less numerous and complex than in males of the same species. However, the extent of the cornual sinus does not vary in any regular fashion with sex. All of these considerations are summarized in Table 6.

DISCUSSION

The major conclusions of the preceding section can be summarized simply: 1. Caprini (male and female) have horns and frontal bones that are relatively larger than are those of the more primitive Rupicaprini. 2. Among the various caprine genera and species, differences exist with regard to the size and shape of the horns, the shape of the skull, and the extent of the sinuses. In the next section we shall discuss the significance of these statements.

GROWTH, DELAYED REPRODUCTION, AND NATURAL SELECTION

Log log plots of various cranial and cornual measurements (FL, CHC, OLHC, and OLHSh) against skull length (VL) have been presented for Rupicaprini (males and females lumped), female Caprini, and male Caprini (figs. 5-7, 14). The slopes of the least square regression lines are listed in Table 7. For each cranial or cornual measurement, the slope is greatest for male Caprini, and least for Rupicaprini. The slope of such a regression line is often a good estimate of relative growth rates (Huxley, 1932; Simpson, 1944), suggesting that the large horns of male Caprini are in part the result of increased growth rates. However, with the exception of frontal length plotted against skull length, the differences between male Caprini and Rupicaprini are not significant at the 0.05 level as indicated by the "t" test (table 8). This situation, we believe, is the result of small sample size and of our having lumped populations which have undergone divergent evolution into the same analysis. Only when the separate species are studied independently will it be possible meaningfully to compare growth rates in male Caprini with those in Rupicaprini. Such comparisons, of course, will require a far greater number of specimens than were available to us.

Despite ambiguities concerning growth rates, it is clear that the horns of Caprini are relatively and absolutely larger than are those of Rupicaprini, and that male Caprini have larger horns than females (table 9). Additionally, male Caprini may be divided into two groups, primitive and advanced, on the basis of horn size relative to skull length (table 9) and skull shape.

TABLE 7.—Cranial and cornual proportions, Rupicaprini and Caprini.

Measurements	Group	N	b	r	P(r)
FL vs. VL	Rupicaprini	7	0.6	0.82	.025
	Caprini females	10	1.1	0.75	.005
	Caprini males	9	1.6	0.84	.0025
CHC vs. VL	Rupicaprini	7	1.3	0.88	.005
	Caprini females	9	1.6	0.84	.0025
	Caprini males	9	2.0	0.91	.0005
OLHC vs. VL	Rupicaprini	7	0.8	0.74	.05
	Caprini females	9	0.9	0.31	—
	Caprini males	9	1.4	0.52	.10
OLHSh vs. VL	Rupicaprini	7	0.7	0.64	.10
	Caprini females	6	1.5	0.74	.05
	Caprini males	9	1.6	0.55	.10

KEY: Measurements of male *P. nayaur* were omitted because of the small size of the sample (1 adult male). N—number of specimens; b—slope of the regression line; r—correlation coefficient for the scatter; P(r)—probability that observed correlation is due to chance.

TABLE 8.—Comparison of the regression slopes from Table 7; male Caprini compared with Rupicaprini; "t" test one-sided. Only FL vs. VL significant at the 0.05 level. d.f.—degrees of freedom.

Measurement	t	d.f.	P(t)
FL vs. VL	2.3	12	< .025
CHC vs. VL	1.5	12	< .10
OLHC vs. VL	0.62	12	< .30
OLHSh vs. VL	0.89	12	< .20

TABLE 9.—Proportions of characters of skulls and horns of male and female Rupicaprini and Caprini.

Group	$\frac{\log FL^1}{\log VL}$	$\frac{\log CHC^2}{\log VL}$	$\frac{\log OLHC^3}{\log VL}$	$\frac{\log OLHSh^3}{\log VL}$
Rupicaprini M.	0.76	0.76	0.80	1.05
Rupicaprini F.	0.74	0.69	0.75	1.00
Prim. Cap. M.	0.84	0.97	1.06	1.16
Prim. Cap. F.	0.79	0.81	0.88	1.17
Adv. Cap. M.	0.97	1.10	1.22	1.44
Adv. Cap. F.	0.85	0.84	0.83	1.11

¹ Caprini primitive for shape of skull are the following: all *Capra*; *H. hylocrius*, and *O. musimon*. The remaining Caprini are advanced.

² Caprini primitive for horn circumference were all *Capra* and all *Hemitragus*.^a

³ Caprini primitive for lengths of horn core and sheath were all *Hemitragus*.^a

^a We believe that *Hemitragus* is not truly primitive for its characters of horn core and sheath, but is probably instead specialized in ways not as yet understood.

The differences between Rupicaprini and primitive males, between primitive males and advanced males, and between Rupicaprini and advanced males are all significant at the 0.05 level as indicated by "t" test.

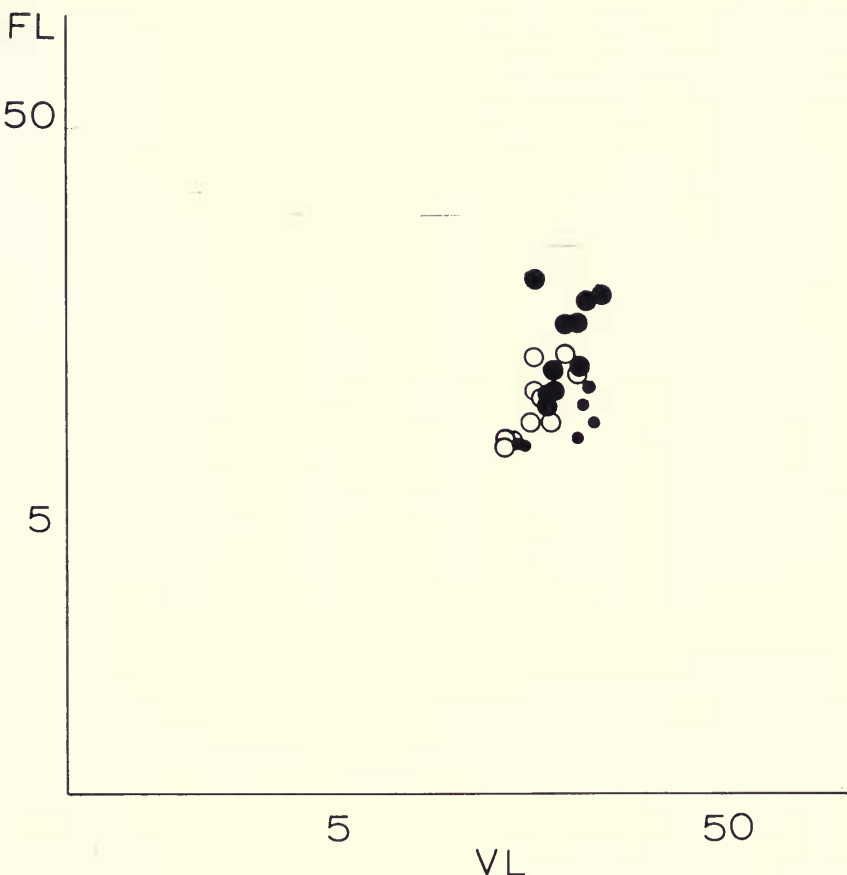


FIG. 14. Frontal length (FL) plotted against length of skull (VL) for Rupicaprini (both sexes, small solid circles), female Caprini (large, hollow circles), and male Caprini (large, solid circles). Log log plot. The slopes of the regression lines are: Rupicaprini—0.6; female Caprini—1.1; male Caprini—1.6; see Table 7.

Increased horn size in males is evidently associated with competition for mates. Among females, there is no such competition and the morphology is little changed from the ancestral Rupicaprine condition. Indeed, female mouflons have lost the horns entirely and those of female *Pseudois* are extremely small. Geist (1966a, 1968a) has observed that among North American mountain sheep increased horn size is correlated with increased mating success inasmuch as the larger (and older) males do most of the mating. There are two reasons for this: first, the females are more inclined to permit mounting by large-horned males, and, second, large-horned males attempt a far

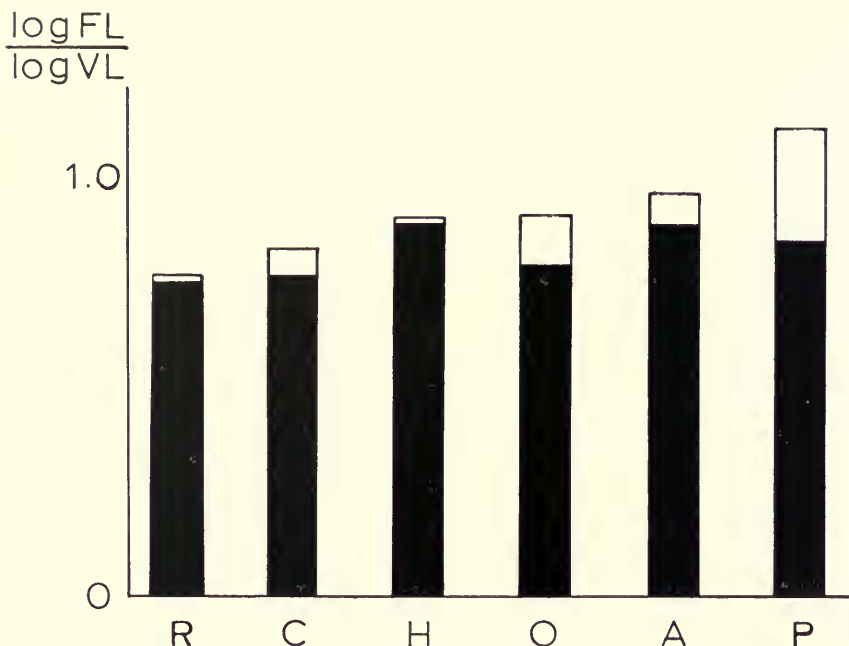


FIG. 15. Ratios of logarithm of frontal length (FL) to length of skull (VL) for Rupicapra and various genera of Caprini. The height of the solid bar gives the values for females; that of the hollow bar, the ratio for males. Note that the amount of sexual dimorphism is generally greater in Caprini than in the Rupicapra.

greater number of copulations. Indeed, young, small-horned rams are so very easily intimidated by the threat displays of males with larger horns that their participation in the rut is minimal. With increasing age and horn size, male bighorn seemingly grow more courageous and by the sixth to eighth year attain behavioral maturity. At this age they can be classified as truly "adult," and participate fully in mating activity. Since male bighorn are sexually mature by the end of the second year (Geist, 1968a), adolescence lasts four to six years. As in human populations, adolescence can be defined as the time between puberty and the attainment of adult morphology and behavioral patterns.

The evolutionary basis of such a social system is grounded in the *potential* for bloodshed and mortal damage inherent in male competition for mates. The fact that students of the animals' behavior report few fatalities resulting from combat should not cause us to lose sight of the fact that the present situation exists as a consequence

of the process of evolution. Natural selection has "chosen" the modifications of behavior which maximize each individual's fitness. In the case of the Caprini, these modifications have masked the potential for mortal combat since subordinate males give way before the threat displays of rivals with larger horns. Fisher (1958) has observed that an animal's fitness, as measured by the number of its offspring, behaves in much the same manner as interest compounded on an investment. Clearly, delaying the date at which a man begins to deposit money in the bank reduces his profit. In a similar fashion, postponing the age of first reproduction—and this is the result of being intimidated by older males—reduces reproductive fitness. To the present authors, it is inconceivable that behavioral patterns resulting in delayed onset of reproductive activities would evolve in the absence of some advantage accruing to the individuals that behaved in this fashion. Such a benefit cannot be discovered if one assumes that intraspecific combat is intrinsically harmless. Much more plausible is the supposition that combat between males of disproportionate size would result in injury or death to the smaller con-

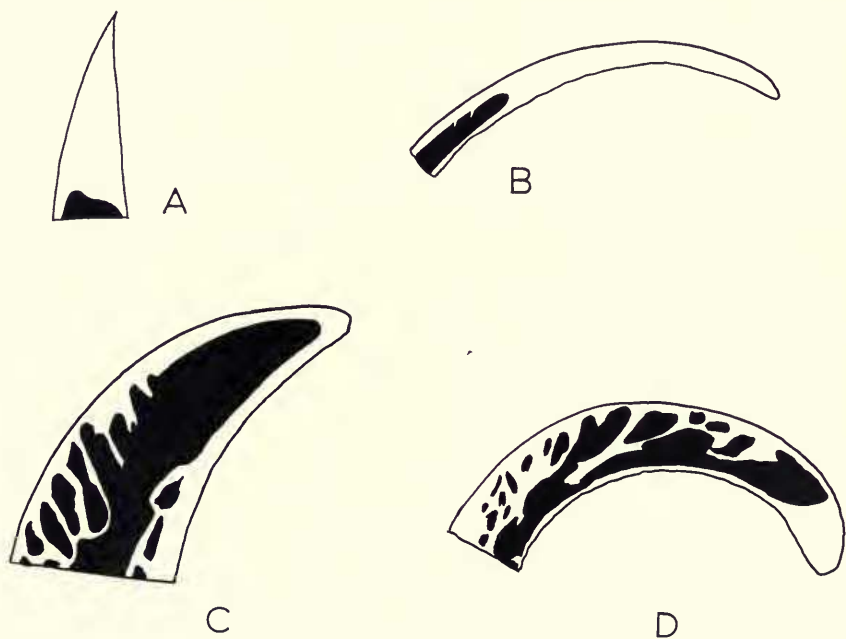


FIG. 16. Sagittal sections of horn cores; sinuses in black. All males. A. *Oreamnos americanus* (Rupicaprini); B. *Capra ibex nubiana*; C. *Hemitragus jemlahicus*; D. *Ammotragus lervia*.

testant. However, such contests are avoided by the behavioral mechanisms discussed above. These considerations can be used to construct a model that predicts optimal reproductive behavior under



FIG. 17. Schematized drawings of primitive and advanced septal configurations in longitudinal sections of horn cores of Caprini. Left—primitive; right—advanced.

a variety of environmental conditions. By “optimal,” we mean the behavioral pattern that maximizes the individual’s fitness. Here we consider r , the malthusian parameter of Fisher, as the most appropriate measure of fitness. We also assume that, among members of a given species, behavioral differences will have a genetic basis and, further, that different behavioral phenotypes will have different fitnesses.

Consider a parameter k which reflects that rate at which a male matures behaviorally. A high value of k means that the animal attempts to compete with older males and mount females at an early age; a low value of k indicates that the animal does not first challenge the dominant males until he is much older. Evidently, k is a measure of a young male’s ability to stand his ground in the face of threat displays by older, larger-horned rivals. Indeed, k is inversely proportional to the length of adolescence. In any population, there will be a distribution of k values among the various animals. Given a genetic basis for these values, it is reasonable to suppose that the modal value of k observed in the population corresponds closely to the optimal value. Any evolutionary innovation, behavioral or morphological, will have a cost and a profit (Gadgil and Bossert, 1970). The fitness of the modification can be expressed by the equation

$$\text{Fitness} = \text{Profit} - \text{Cost} \quad (1)$$

In the case of selection for optimal k , we write

$$\text{Fitness} = P(k) - C(k) \quad (2)$$

where $P(k)$ is the profit and is a function of k and $C(k)$ is the cost and is also a function of k . Since fitness is also a function of k , we seek to determine the value of k that maximizes the expression $P(k) - C(k)$. We have observed, as have also Cole (1954) and Gadgil and Bossert (1970), that fitness decreases when the age of first reproduction is increased. This decrease will be our cost function $C(k)$. At $k=0$, $C(k)$ is infinite because the organism never reproduces; at $k=\infty$, $C(k)=0$ because the animal reproduces as soon as he is physiologically capable. $C(k)$ will thus be a decreasing function asymptotically approaching zero as k approaches ∞ (fig. 18). If there is no

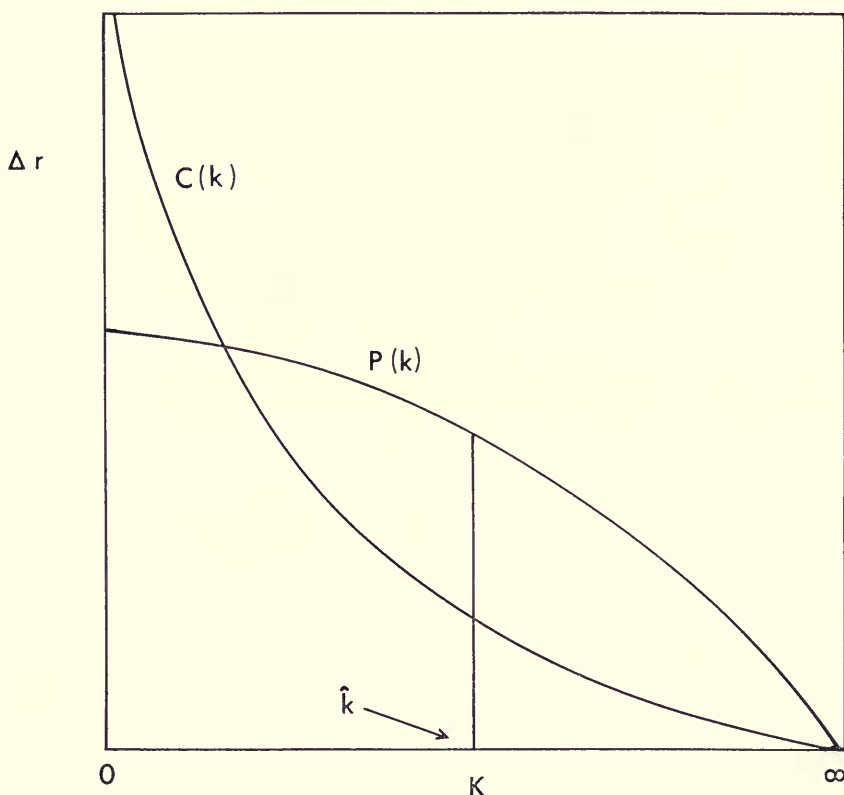


FIG. 18. Cost, $C(k)$, and profit, $P(k)$, functions, plotted against k . k is proportional to the rate at which a male matures behaviorally. Fitness (Δr) is maximized when $P(k) - C(k) = \text{maximum}$. \hat{k} is the value of k that maximizes r . See text for further explanation.

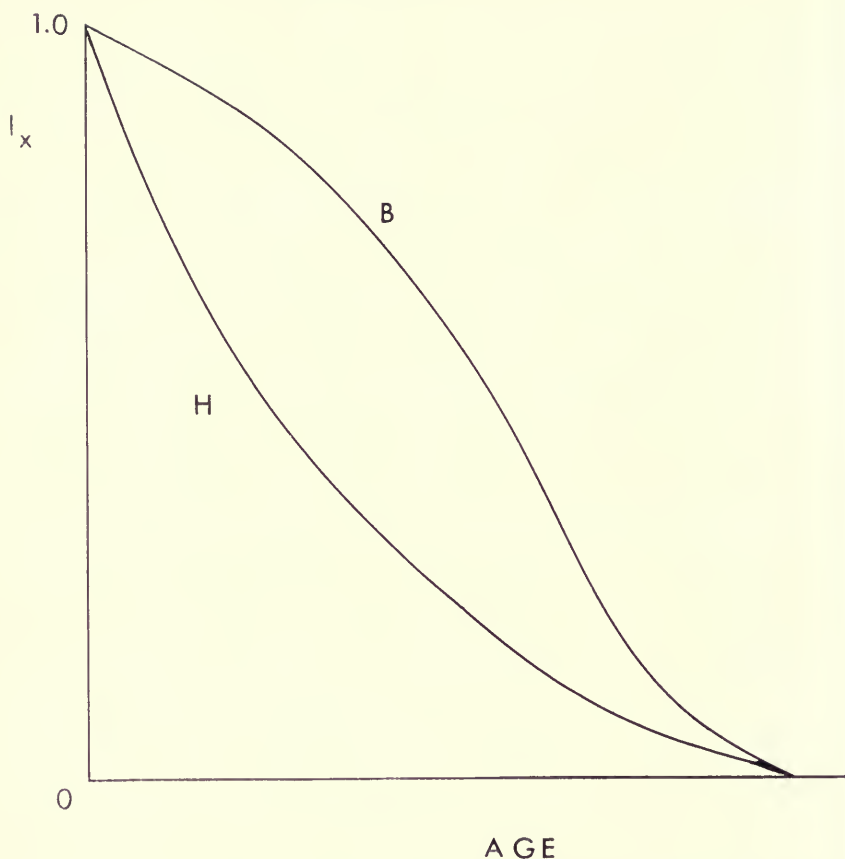


FIG. 19. Survivorship curves in harsh (H) and benign (B) environment. l_x is the probability that an animal will live to age x .

profit for delaying the first reproduction, equation 2 will be maximized at $k = \infty$. This is the case for female Caprini which do not compete for mates, and it is not surprising that female mountain sheep begin reproducing shortly after the onset of puberty. In males, however, there is a profit function. Increasing k lowers the age of first reproduction and increases the possibilities of fatal contests between younger rams and the larger males. Decreasing k reduces the possibility of such encounters. Since males essentially cease growth by the eighth year, reducing k below the value that indicates first reproduction at this age does not further increase $P(k)$. Accordingly, when plotted against k , $P(k)$ will be finite and essentially constant for low values of k and then decline to 0 as k ap-

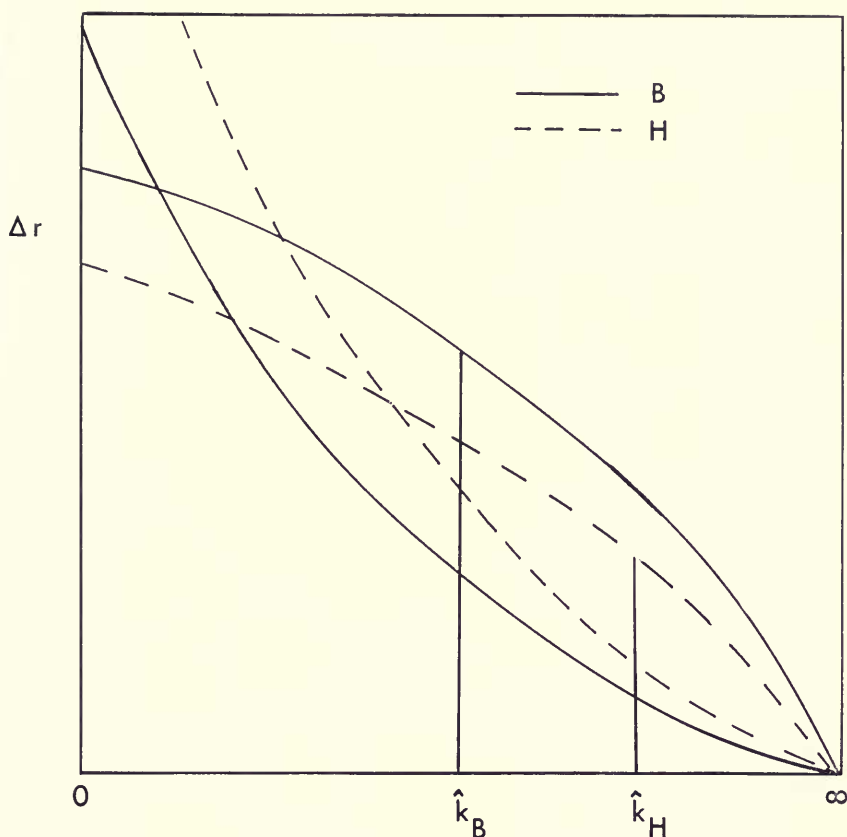


FIG. 20. k is obtained for harsh (H) and benign (B) environments. In the harsh environment r is greater (\hat{k}_H) than in the benign one (\hat{k}_B).

proaches ∞ (fig. 18). Plotting profit and cost functions together, we obtain Figure 18. The value of k that maximizes the difference between $P(k)$ and $C(k)$ is denoted \hat{k} . This is the optimal value of k . Notice that if $P(k)=0$ for all k , $\hat{k}=\infty$. This, we observed, was the predicted value of k for females.

We now inquire into the effect of varying environmental harshness on \hat{k} . The term "environmental harshness" is defined in terms of a population's survivorship curve (Deevey, 1947). Obviously, an environment that is harsh for one species may be perfectly hospitable for another. Again, an environment adjudged harsh by one scientist may not be so judged by another. We shall take the shape of the survivorship curve as a measurement of harshness. A harsh environment is one in which the survivorship curve falls off steeply; in a

TABLE 10.—Observed behavior, morphology, and environmental harshness for various populations of Rupicapriini and Caprini.

Population	M.C.	\bar{X}		$X_{max.}$		H		A		$A/X_{max.}$		H.S.	
		♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀
RUPICAPRINI													
<i>Oreamnos americanus</i>	NO	—	—	—	—	—	—	2.5	2.5	—	—	0.8	0.8
<i>Rupicapra rupicapra</i>	YES	3.0	4.2	18	18	.83	.76	3.0	2.0	.12	.11	1.6	—
CAPRINI													
<i>Ovis aries</i> (Soay)	YES	1.3	3.6	10	14	.87	.74	0.5	0.5	.05	.04	1.4	—
<i>Hemitragus jemlahicus</i>	YES	—	3.5	—	18	—	.80	4.0	2.5	.23*	.15	1.4	1.1
<i>Ovis canadensis</i>	YES	5.2	4.6	16	14	.68	.68	7.0	2.5	.42	.18	2.3	0.8
<i>O. musimon</i>	YES	3.3	3.5	10	14	.67	.75	4.0	2.0	.40	.14	2.3	—**

* $X_{max.}$ of the females was used in the absence of data for the males.

** The females are hornless in this population.

KEY: M. C.—mate competition among males; \bar{X} —average age; $X_{max.}$ —maximum age; H—environmental harshness; A—average age of first reproduction; H.S.—horn size (i.e., relative development of the horn).

Survivorship data from Couturier (1949) for *Rupicapra*; Boyd et al. (1964) for *Onis aries*; Caughley (1966) for *Hemitragus*; Murie (1944) for *Onis canadensis*; and Pfeffer (1967) for *Onis musimon*.

Data on age of first reproduction from Couturier (pers. comm.) for *Rupicapra*; Grubb (pers. comm.) for *Onis aries*; Caughley (pers. comm.) for *Hemitragus*; Geist (1968) for *Onis canadensis*; and Pfeffer (1967) for *Onis musimon*.

Horn measurements on Soay sheep taken by Reed with permission of Peter Jewell.

benign environment, the curve falls off more gently (fig. 19). As an index of shape of the survivorship curve we will use the statistic

$$H = 1 - \frac{\bar{X}}{X_{\max.}}$$

where \bar{X} is the expected lifespan of an individual and $X_{\max.}$ is the maximum life expectancy. If all individuals survive to their maximum age, $H=0$. This is the least harsh environment conceivable; if nearly all the individuals die just after birth, $H=1$, the harshest possible environment. H will clearly be affected not only by physical factors—average temperature, rainfall, etc.—but also by biological factors—competition, predation, parasitism, etc.—and, in addition, by factors peculiar to the physiology and behavior of the species in question. In Figure 20, the effects of increasing H on $P(k)$ and $C(k)$ are shown. If males have little probability of living to an old age regardless of their reproductive behavior, $P(k)$ —the increase in survivorship resulting from avoiding the rut—will be reduced because there will be fewer older males to injure aggressive adolescents. The cost function, $C(k)$, on the other hand, will be increased by reducing k , for the very reason that delay will more likely mean that the individual will not reproduce at all. As a result, \hat{k} will be greater in harsh environments than in benign ones. Stated another way, we expect the age of first reproduction of males to decrease with increasing environmental harshness.

Survivorship data for large mammals are difficult to obtain. However, for Caprini, life tables of reasonable accuracy are available for *Ovis canadensis* (Deevy, 1947; Murie, 1944); for *Hemitragus jemlahicus* imported into New Zealand (Caughley, 1966); for feral Soay sheep (*Ovis aries*) on the island of Hirta, St. Kilda, on the western fringe of the Outer Hebrides, Scotland (Boyd et al., 1964); and for *Ovis musimon* (Pfeffer, 1967). In addition, Couturier (1949) gives life table data for the rupicaprine *Rupicapra rupicapra*. In Table 10, we have recorded the following data for these populations: H , \bar{X} , $X_{\max.}$, A (the age at first reproduction), and $A/X_{\max.}$ (the relative age of first reproduction). In Figure 21, we have plotted H against $A/X_{\max.}$ for both males and females. In accordance with our prediction, the relative age of first reproduction among males declines with increasing environmental harshness. No such pattern is visible among the females. Changes in male reproductive behavior are most dramatically illustrated by the Soay sheep. In this popula-

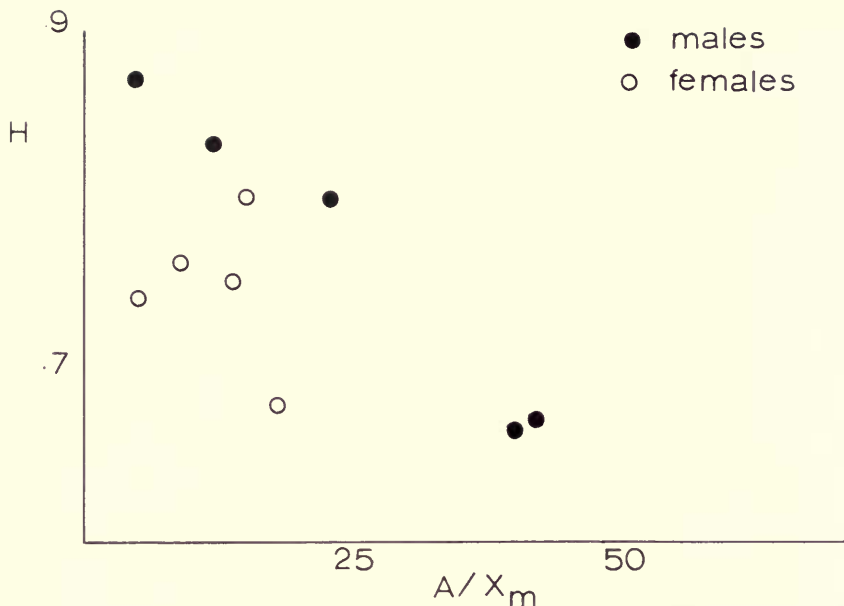


FIG. 21. Environmental harshness, H , plotted against the relative age of first reproduction, A/X_m ($X_m = X_{max.}$), for different populations of Caprini and Rupicaprini. Among males, increasing environmental harshness is associated with an earlier age of first reproduction. The correlation coefficient, $r = .98$; $P(r) < .005$ (one-sided). No such trend is apparent among females.

tion, the male lambs attempt to participate in the rut, both running with the mature rams and attempting copulations (Boyd et al., 1964; Grubb, personal communication). Indeed, Grubb (personal communication) reports that these lambs are subjected to quite vicious attacks by the older males. Clearly, they are not so easily intimidated by the threats and attacks of the adults as are the young American bighorn studied by Geist (1966a). The low survivorship rates of male Soay sheep are due both to the limited grazing area available on the island and the presence of an internal parasite which periodically decimates the population. Most susceptible to the parasite are the yearling rams. Thus, selection for attempted copulation by lambs is quite understandable. Contrast this situation with that of the mouflons studied by Pfeffer (1967). Although the two species are quite closely related, survivorship is higher in the males of wild mouflons, where $H = .67$, than in Soay males ($H = .87$). Associated with increased survivorship, is an increase in the relative age of first reproduction ($A/X_{max.} = .40$ vs. $.05$ for Soay males), a correlation which our theory predicted.

In the tahr the situation is less clear. Published studies of behavior are entirely lacking, and Caughley's estimate of the modal age of male reproduction must be viewed with some caution. Also, the only available survivorship data are for females, and we must admit to the possibility that these do not closely agree with the male data, which have never been collected. Nonetheless, we work with what we have and the agreement between the predictions of the theory and the observations on the populations is encouraging.

Further confirmation of the theory is provided by Geist's observations (1964) of the rupicaprine *Oreamnos americanus*, the Rocky Mountain "goat." In this species, the horns are but slightly curved and end in sharp tips. This fact makes fighting between rival males a potentially lethal proposition for both contenders no matter what the size differential between them. The usual result of the rare fights that do occur is the sustaining of extremely damaging puncture wounds. As a result, it does not "pay" an adult male to fight even a juvenile as the chances of injury are so great. Predictably, there is little or no fighting between males. Indeed, Geist has observed that adult males are subdominant to yearlings and females. Since older males do not attempt to exclude their younger rivals from the rut, the profit function $P(k)$ is 0 for all k . One then expects the males to reproduce as soon as physiologically possible, which indeed they do, as both males and females first reproduce at $2\frac{1}{2}$ years.

Growth is the opposite side of the coin we have been discussing. Energy devoted to increased horn size must be diverted from some other function. The usual correlates are decreased survivorship or fecundity. This diversion of energy is the cost function and will be selected for only if there is an associated profit—in this case increased effectiveness in combat and display. As horn size increases, the profit function levels off and becomes constant when the horns are sufficiently large to enable their bearer to defeat or intimidate most of his rivals. The cost function, on the other hand, continues to increase at all horn sizes. Thus, an optimal horn size is determined.

The profit and cost functions associated with increased horn size are affected by environmental harshness in much the same way that the profit and cost associated with delayed reproduction are affected. In a harsh environment, the profit is diminished—because there will be fewer older, large-horned males with whom to compete. Similarly, because life expectancy is diminished, the cost of any given diversion of energy will be increased. As a result, we predict smaller

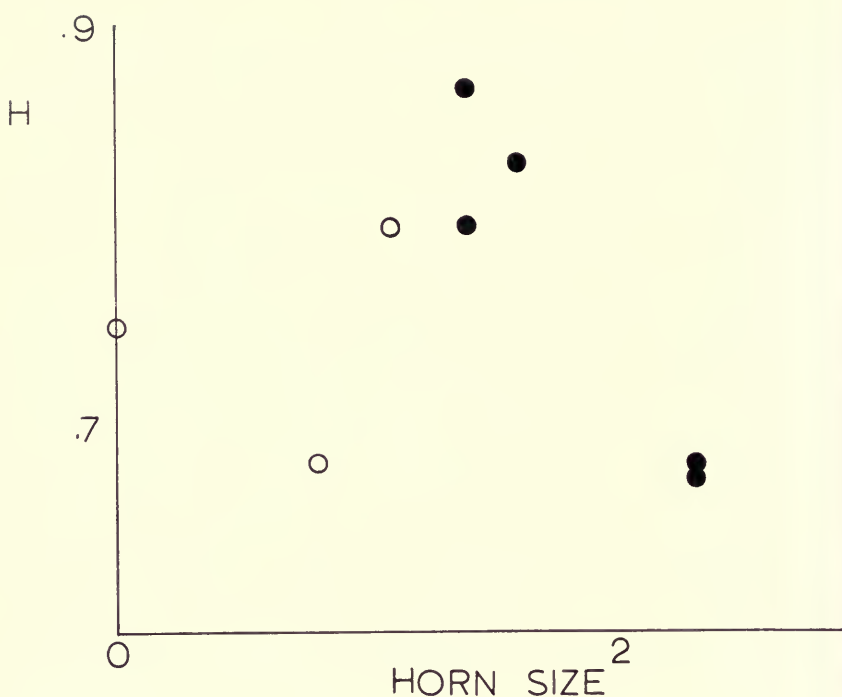


FIG. 22. Environmental harshness (H) plotted against relative horn size for different populations of Caprini and Rupicaprini. Among males, horn size decreases with increasing harshness. $r = .95$; $P(r) < .01$ (one-sided). Among females, no such trend is apparent.

horns in a harsh environment. As a measure of horn size, we use the statistic H.S., which is defined by the relation

$$H.S. = 1/2 \left(\frac{O.L.H.Sh. + C.H.C.}{V.L.} \right)$$

Values of H.S. are included in Table 10. In Figure 22, we have plotted H.S. against H, our measure of environmental harshness, for both males and females of different Caprini and Rupicaprini. In accordance with the prediction, increased environmental harshness is associated with smaller horns in the males. Among females, there is no such pattern. This situation is to be expected since the females do not use the horns to fight with each other for mates. Indeed, the functions of the horns in female Caprini remain unclear to us. Associated with the relatively larger horns of male Caprini is increased sexual dimorphism with regards to both horns and skulls. In general, Caprini are more highly dimorphic than Rupicaprini (table 11).

TABLE 11.—Values of sexual dimorphism, Rupicaprini and Caprini.

Species	VL	FL	CHC	OLHC	OLHSh
<i>Nemorhaedus goral</i>	— .01	0	.23	.14	.06
<i>Capricornis sumatrensis</i>	.01	.08	.09	.16	.17
<i>Oreamnos americanus</i>	.11	.09	.28	.19	.02
Average Rupicaprini	.04	.04	.20	.16	.08
<i>Capra hircus aegagrus</i>	.23	.26	.56	.73	.72
<i>C. hircus hircus</i>	.14	.30	.52	.57	.62
<i>C. ibex sibirica</i>	.14	.28	.50	.67	†
<i>Hemitragus hylocrius</i>	.09	.16	.30	.30	.22
<i>H. jemlahicus</i>	.13	.19	.36	.44	†
<i>Ammotragus leervia</i>	.12	.28	.42	.41	.45
<i>Pseudois nayaur</i>	.03	.58	.70	.80	†
<i>Ovis musimon</i>	.15	.24	1.00*	1.00*	1.00*
<i>O. canadensis</i>	.14	.37	.64	.69	.73
<i>O. ammon</i>	.14	.38	.62	.70	.60
Soay Sheep**	.04	.13	.34	.72	
Average Caprini	.12	.29	.54	.64	

KEY: The index of dimorphism for each measurement, X, is given by the

$$\text{formula } \frac{x_m - x_f}{x_m} = \text{index of sexual dimorphism.}$$

* Females hornless.

† Females with horns sheaths not available.

** Hornless females excluded.

This, we feel, reflects both increased survivorship and a greater tendency to joust strenuously with the horns. Male Rocky Mountain goats, as we have previously noted, do not fight at all—hence the similarity of horn structure between males and females. Of the other Rupicaprini, behavioral and life historical data exist only for *Rupicapra rupicapra* (Couturier, 1938, 1949). The males of this species do fight with each other and use their horns for this purpose. However, fighting is less intense than in Caprini and survivorship is considerably lower ($H=.83$). The relatively small size of the horns in the males and the early age of first reproduction agree with these observations.

In closing this section, we would like to observe that the harshness or benevolence of an environment is a function not only of extrinsic factors—the physical and biological environment—but also of the morphology and behavior of the animals in question. In addition to cranial specialization, the Caprini have evolved remarkable talents for climbing, jumping, and running. These, coupled with their relatively large size and preference for mountainous habitats,

have undoubtedly reduced predation pressures on healthy adults. In essence, it is possible that becoming adapted to live in the mountains with grace, enabled the Caprini to increase their survivorship and thus convert a harsh world into a benevolent one. Such a conversion would then pre-adapt the animals for evolutionary paths that led to delayed reproductive patterns in males and the growth of splendid horns. In our view, then, delayed reproductive behavior can evolve without the development of the type of harem system such as is observed in sea lions, deer, and some antelope. These social systems do, of course, also involve an unwillingness on the part of young males to challenge the dominant males. Unfortunately, the conditions that led to the evolution of a caprine type social system as opposed to a harem system with its concomitant territoriality remain unclear to us.

PREVENTION OF BRAIN DAMAGE

Thus far, we have dealt with generalities: growth and its adaptive significance in the context of a species' behavior and ecology. We now turn to some specifics which, while perhaps more mundane to the evolutionist, are of the utmost importance to a ram contemplating intraspecific combat. The first of these topics concerns the prevention of damage to the brain. Caprini appear to be protected against two, and possibly all three, of the following causes of head injury: 1. Inbending of the bone surrounding the brain; 2. angular acceleration of the skull; 3. linear acceleration of the skull. We shall consider each of these potential sources of injury and the means by which their realization is prevented in the Caprini.

The most obvious result of impact to the calvarium is fracture. However, actual breaking of bones is not necessary to produce concussion and even death, since local, reversible inbending can generate transient increases in pressure throughout the brain cavity. Because the skull is much more rigid than is the spinal tube,¹ increased intracranial pressure will cause fluid to flow out of the braincase and into the spinal tube. Such flow generates shear stresses in the region of the cranio-spinal junction (Gurdjian and Lissner, 1961; Edberg et al., 1963) which result in lesions in this area. In addition, the snap-back of the bone will produce local negative pressures that may be accompanied by cavitation and destruction of nerve tissue and blood ves-

¹ The dura mater which encloses the spinal contents is free to expand between the vertebrae if the fluid pressure within the tube is increased.

sels. Finally, impact of sufficiently great force will momentarily compress the entire skull, generating shear stresses in the interior of the brain and causing destruction of tissue in this region as well.

In all Caprini observed, at least some of the blows land on the forehead, which means that impact occurs on the frontal bones. But these have been divided into two layers of bone with an intervening air sinus. Compression of the outer layer will not necessarily result in compression of the inner layer which surrounds the brain. Geist (1966a) has pointed out that frontal sinuses are common in many animals that butt with the head. The protection against deformation of the calvarium afforded by such sinuses would appear to be their *raison d'être*. In species such as *Ovis canadensis* in which the force of impact is great, the outer layer of the frontal bones is buttressed by the septa within the sinus. Thick, regularly shaped septa would, of course, transmit deformation of the outer layer to the braincase. It is significant that in all Caprini the septa are thin and shaped irregularly. Unterharnscheidt (personal communication) has suggested that the septa act as springs to cushion the blow by undergoing slight deformation themselves. Such a mechanism is quite reasonable, but can only be tested by experiments on freshly-killed material which was unavailable to us.

Rotation of the skull about the cranio-spinal junction is a second possible source of injury. Holbourne (1945) demonstrated that in man such rotation will produce shear stresses within the brain mass. Unterharnscheidt and Higgens (1969) have pointed out that angular acceleration will also cause the brain to rotate relative to the inner wall of the braincase, causing superficial lesions and the tearing of nerves and blood vessels. Pudenz and Sheldon (1946) observed such rotation in monkeys whose calvaria had been replaced with lucite domes. In a previous publication, one of us (Schaffer, 1968) pointed out that the development of the neck muscles in the various Caprine species is proportional to the magnitude of the torque resultant from impact. The implication is that Caprines resist rotation of the skull by contracting the neck muscles during impact. While the development of the neck muscles is important in this regard, attention also needs to be given to the shape of the skull. In goats, the skull is primitive. The brain protrudes behind the bases of the horns. Since impact occurs far out on the horns (fig. 23), a torque will be generated that will cause rotation about the occiput in a clockwise direction. Accordingly, the neck muscles and their areas of insertion of the skull are quite large. If the skull shape were advanced, i.e., if the foramen magnum were beneath the horn bases, the torque

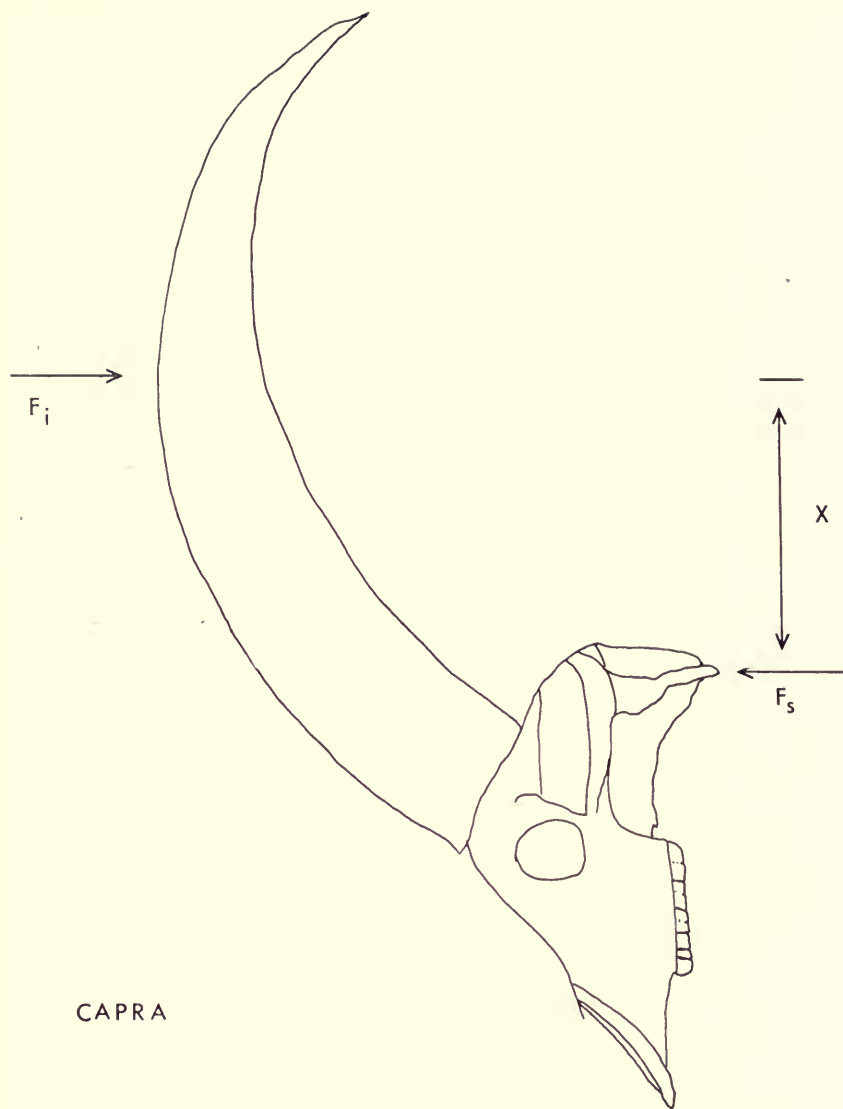


FIG. 23. Impact in *Capra*. The impact vector F_i is displaced from the support vector of the neck (F_s), by the lever arm X . Notice that if the skull configuration were of the advanced type, the condyles would underlie the horn bases and X would be larger. (After Schaffer, 1968.)

would be much greater in magnitude. The retention of the primitive skull pattern in goats is, we believe, correlated with the fact that impact occurs far out along the horns. Alteration of the skull shape in the direction of the more sheep-like Caprini would needlessly lengthen the lever arm, hence requiring the presence of even larger neck muscles to counter the increased rotary torque. We should also observe that crossing relatively narrow horns is an effective way of receiving a blow only if the force of impact is relatively low. In advanced Caprini, on the other hand, the force of impact is presumed to be much higher than in the goats (Schaffer, 1968). As a result, the horns are much broader and in *Ovis* and *Ammotragus* impact occurs near the bases of the horns. In this case, impact would tend to rotate the skull counterclockwise if the skull shape were still primitive. Of course, it is not (fig. 24), and we would suggest that the adaptive significance of the advanced skull configuration lies in the fact that it brings the supporting column of the neck in line with the vector of impact, thus reducing the magnitude of the rotary torque. Placement of the vertebral column in line with the force of impact also provides more efficient support for the skull. This is of particular importance in the larger sheep in which the force of impact may be as much as three to four times that in goats of corresponding size. Thus, the point of impact, which is a function of the placement and spiral angle of the horns, is correlated not only with the development of the neck muscles, but also with the shape of the skull and the magnitude of the force of impact.¹

A third possible source of damage to the brain is linear deceleration. For a braincase whose diameter in the direction of impact is 5–8 cm., decelerations causing 350–500 G will produce a complete vacuum in the region of the brain opposite the point of impact (Sellier and Unterharnscheidt, 1963). Among the larger sheep, the deceleration caused by impact may indeed approach this figure. The change in velocity may be as much as 1400 cm./sec. (=30 mph) but the time interval during which this occurs has not been determined. If the horn and septa act as cushioning devices, one would expect the deceleration time to be rather long (say several milliseconds) in which case the maximum tolerable limit would not be exceeded. On the other hand, it may be that male sheep do sustain brain damage

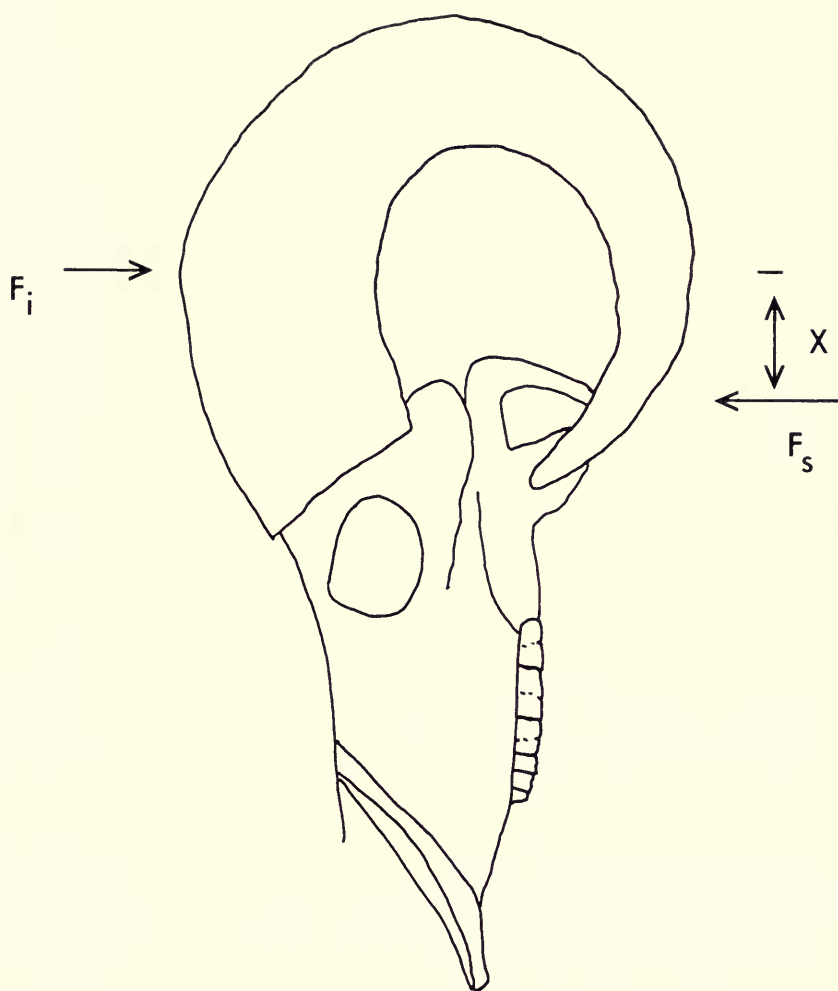
¹ An apparent exception to these remarks is *Pseudois*, in which impact occurs about half way along the horns. These, it will be recalled, diverge from each other at an angle approaching 90° so that the points of impact and the support vector of the neck are roughly coplanar. As in *Ovis* and *Ammotragus*, a primitive skull shape would result on impact in the production of counter-clockwise torques about the occiput.

during combat which in the long run proves injurious. The resolution of this problem, however, will come only after experimentation far beyond the scope of this study. We do emphasize that in species of Caprini that do not charge their opponents at high speed—the goats, *Ammotragus*, and probably *Hemitragus*—the change in velocity will be insufficient for linear deceleration alone to cause brain damage, cushioning or not.

FIGHTING STYLE AND THE SHAPE OF THE HORNS

In the section on behavior, we observed that in *Ovis* and *Ammotragus* (and probably also in *Pseudois*) impact is frontal and usually horn to horn. In goats, on the other hand, the horns are crossed and the animals' heads are tilted at the moment of impact, producing rotational torques in the transverse and sagittal planes (Schaffer, 1968). Such torques are not generated when impact is frontally directed and it is not surprising that in species in which the males actually charge each other (thus increasing the magnitude of the impact force) the approach is as directly head-on as the two antagonists can co-operatively produce. In such cases, obviously, it is important that the contestants not slip past each other and violently wrench their necks. Correlated with horn-to-horn butting are broad frontal surfaces (fig. 4; table 9), and, in the cases of *Ovis* and *Ammotragus*, impact near the bases of the horns where they are broadest. In *Capra*, on the other hand, the horns are crossed on impact. In this case, broad horns are superfluous. Predictably, the horns of *Capra* are relatively and absolutely more narrow than those of *Ammotragus*, *Pseudois*, and *Ovis*.

In addition to the effects of interspecific differences in fighting style, one can also consider the effects of butting behavior in a more general sense. For example, the horn core, like any other structure, can be expected to be designed efficiently. Like a beam attached at one end and loaded at the other, efficient design means constructing the horn core in such a way that the ratio of the compressive and tensile stresses equals the ratio of the compressive and tensile strengths. Bone is stronger in compression than in tension (Evans, 1957). Accordingly, we expect the horn core to be shaped in such a way that the maximum compressive stresses exceed the maximum tensile stresses. Figure 25 illustrates a beam anchored at one end and loaded at the other (L). The fibers near the top of the beam are stretched; those near the bottom compressed. Within the beam is a layer of fibers in the neutral axis (n), in which the fibers are neither stretched nor compressed. In a straight beam the neutral axis cor-



OVIS

FIG. 24. Impact and support vectors in *Ovis*. Impact is to the bases of the horns and the impact and support vectors are nearly co-linear. Retention of the primitive skull pattern would place the condyles behind the point of impact and would generate a counter-clockwise torque. (After Schaffer, 1968.)

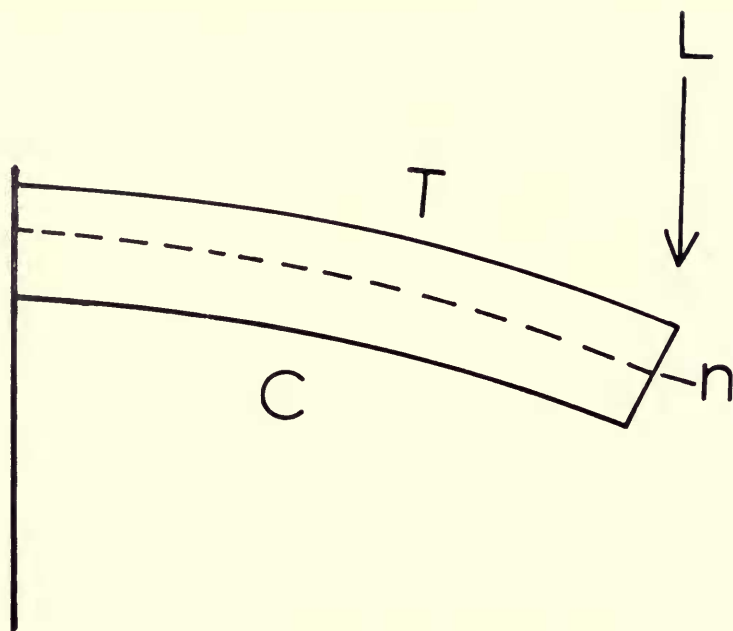


FIG. 25. Compressive and tensile stresses in a loaded cantilever beam. The loading (L) is at the end of the beam. Within the beam, bending stresses of tension (T) and compression (C) are generated. Along the neutral axis (n), the fibers are neither stretched nor compressed. The magnitude of the stresses increases with distance from the neutral axis.

responds to the line joining the centroids of successive cross-sections. In a curved beam (fig. 26), the neutral axis lies below the centroidal axis. The distance—denoted by “e” in the figure—is a function of the shape of the beam’s cross-section and the upper and lower radii of curvature. The magnitude of stresses induced by loading increases with distance from the neutral axis. As a result the maximum stresses occur along the edges of the beam. Also, the position of the centroid affects the relative magnitude of the compressive and tensile stresses. For a straight beam, the ratio of compressive to tensile stress is given by the equation

$$\frac{\sigma_c}{\sigma_t} = \frac{h_1}{h_2} \quad (1)$$

where h_1 is the distance from the centroid to the bottom of the beam and h_2 the distance to the top of the beam (fig. 26). For a curved beam, expression (1) is complicated by the effect of the differing radii

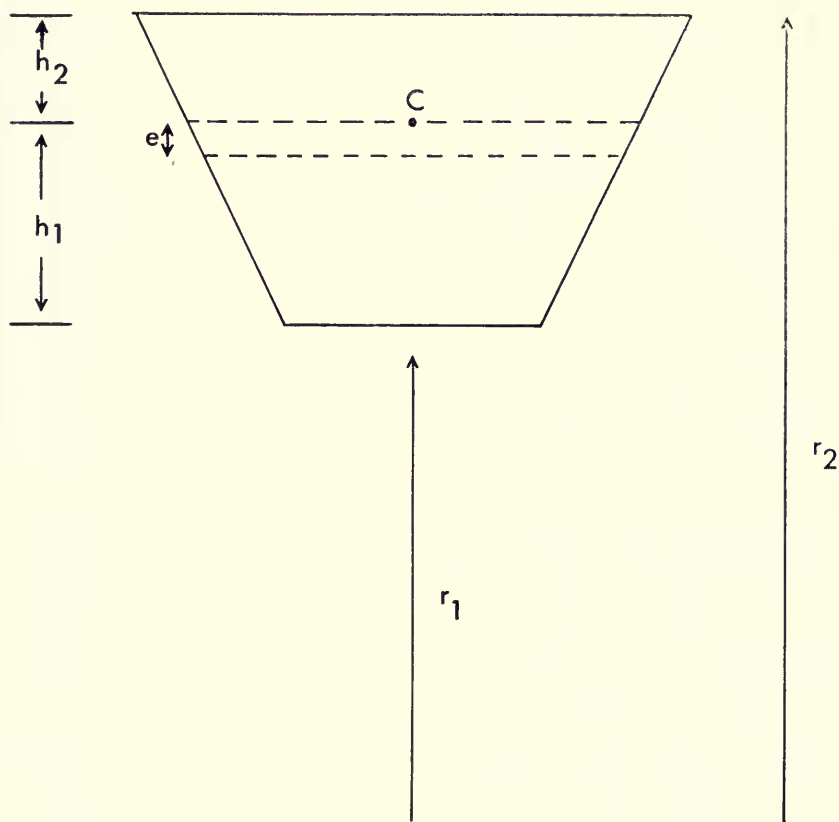


FIG. 26. Cross-section of a curved cantilever beam. C is the centroid, which is located at the center of mass. Because the beam is curved (down in this illustration), the neutral axis is displaced below the centroid a distance e . h_1 is the distance from the centroid to the bottom edge of the beam; h_2 , the distance to the top edge. The radius of the top edge is given by r_2 ; that of the bottom edge by r_1 .

of curvature of the top and bottom edges of the beam. In this case, the ratio of stresses is given by the expression

$$\frac{\sigma_c}{\sigma_t} = \frac{h_1 - e}{h_2 + e} \cdot \frac{r_1}{r_2} \quad (2)$$

where r_1 is the inner radius of the beam and r_2 the outer radius (Timoshenko and Young, 1968); e is the distance between the centroidal axis and the neutral axis.

In an unpublished study, one of us (Schaffer) determined the position of the centroids of basal cross sections of 12 caprine horn cores (table 12). As a result, it was possible to measure h_1 and h_2

TABLE 12.—Ratios of maximum compressive to maximum tensile stresses in the horn cores of Caprini.

Genus	N	r ₁	r ₂	h ₁	h ₂	e	$\frac{\sigma c^*}{\sigma t}$
<i>Capra</i>	3	28.0	35.2	2.9	2.6	0.1	1.27
<i>Hemitragus</i>	1	12.9	18.3	4.9	4.5	0	1.55
<i>Ammotragus</i>	2	13.1	18.6	3.1	2.5	0.2	1.61
<i>Ovis</i>	6	10.5	19.8	4.9	4.3	0.6	1.70
Average							1.56
Std. dev.							0.17

KEY: N—number of specimens; other measurements are defined in Figures 25, 26.

* The ratio of stresses was computed for each specimen and these averaged for each genus.

The ratios of the stresses for all 12 specimens were computed and averaged; the standard deviation was also based on the ratios for the individual specimens.

as well as the radii of curvature; e was calculated from the shape of the cross-section. These data were then used to compute the ratio of stresses in each specimen (table 12). The results were in striking agreement with the ratio of ultimate strengths in compression and tension calculated for fresh bone (Evans, 1957). The ratio of the stresses was 1.56 (std. dev.=0.17); that of the strengths, 1.57 (std. dev.=0.31). This result must be viewed with caution, however, since the analysis is only valid if loading (in this case impact during butting) is quasi-static; that is the time during which the horn is loaded, i.e., the length of time that the opponents' horns are in contact, greatly exceeds the time it takes the shock produced by impact to travel down the horn to its base and back to the point of contact. In addition, it is assumed that relative to the stresses produced by bending, shear stress is negligible. Preliminary investigations indicate that this is probably true for *Capra* and *Ammotragus*. In *Ovis*, however, the force of impact is greater than in the other genera, and the point of impact closer to the base. Actual measurements of impact times and forces will be necessary to determine the applicability of the computations to this genus.

The fact that the stresses placed upon the horn by ramming so greatly exceed all others suggests additional studies which make use of the methods of structural design. The optimal stiffness of the horn, the resistance to shearing, and the means by which the energy of impact is dissipated are but three. All of these, however, require more detailed knowledge of the nature of impact than is now available.

We shall close this section with a single observation concerning the orientation of the septa within the horn core. Reference to Fig-

ures 16 and 17 shows that most of the septa lie along the lines of principal stress, which because of the curved shape of the core are mostly lines of compression. Such orientation gives maximum strength while utilizing a minimum of material. It should be noted that this sort of arrangement of bone has also been observed in the human femur and calcaneum (Thompson, 1945). Its presence in the horn cores of Caprini is therefore not surprising inasmuch as these structures are subjected to far greater loading forces.

SUMMARY AND CONCLUSIONS

A study of the agonistic behavior and cranial anatomy in the sheep and goats (bovid tribe Caprini—*Capra*, *Hemitragus*, *Ammotragus*, *Pseudois*, and *Ovis*) reveals the following patterns characteristic of the group: 1. An emphasis on head-to-head butting or ramming as a major form of intraspecific competition between adult males as a prelude to mating; 2. Lack of harem formation, but exclusion of sexually competent juvenile and adolescent males from the rut by the intimidative activities of mature males in populations with high survivorship rates; 3. Great increase in the size of horns and horn cores in the males; 4. Concomitant increase in the size and complexity of the frontal and cornual sinuses and an increase in the complexity of the septa within these cavities; 5. An associated alteration in the shape and relative proportions of the skull, the changes being particularly profound in those species in which the force of impact is great and directed to the bases of the horns.

The evidence indicates that the different characters, behavioral and morphological, evolved together as an adaptive complex. Females do not compete for mates by butting and ramming each other, and do not have large horns, nor do they exhibit the delayed reproductive patterns characteristic of the males. Additionally in females, the shape of the skull and the extent and complexity of the sinuses and septa have remained primitive. By contrast, the living Rupicaprini, presumed to resemble closely the antecedents of the sheep and goats, are characterized by body butting (a pattern observed in juvenile sheep, but only infrequently in adults—Geist, 1968b), and little or no increase in size of the horns, sinuses, and septa. The shape of the skull is similar to that of caprine females and to that of the most primitive male Caprini. Little is known concerning the age at which Rupicaprine males first attempt copulation with estrous females, except in *Rupicapra rupicapra* where the first reproduction is delayed less than in mountain sheep and tahr. This agrees with the fact that survivorship in Chamois is lower than in the aforementioned Caprini.

In Rocky Mountain goats (*Oreamnos americanus*) fighting between males of disproportionate or equal size has been selected

against because of the injurious effects to both contestants produced by penetration of the sharp horns into the body. Predictably, the males do not compete with each other during the rut nor do they delay their first entry into the rut beyond the age at which they first become sexually mature. Male bighorn, on the other hand, become sexually mature at about the same age as the mountain goats (two to three years), but delay their first entry into the rut until the sixth to eighth year. This fact, we believe, is associated with the observation that male sheep will fight with each other in the manner described earlier in this paper. Such agonistic behavior is possible, we think, because an older male can defeat a younger rival without risking injury. In general, male Caprini are distinguished by curving horns that permit head-to-head butting and ramming that will not result in injury to the larger animal. The evolution of a curved horn is very likely the adaptation upon which subsequent changes in horn size and reproductive behavior are based.

Within the Caprini, the configuration of the skull has remained primitive in those species in which the force of impact is low. In contrast, *Ammotragus*, the larger sheep and presumably *Pseudois* ram each other with much greater force and have evolved a new skull shape in which the foramen magnum is rotated to a point below the site of impact. The brain is protected from damage by several adaptations which include increased extent of the cornual and frontal sinuses and the septa within, and again by the placement of the supporting column of the neck vertebrae in line with the impact vector. In goats, rotation of the skull about the occiput at the second of impact is prevented by contraction of the neck muscles which are relatively larger than in species with advanced skull shapes.

The correlated morphological and behavioral differences between the living genera of Caprini, and particularly those between *Capra* and *Ovis*, lead us to reject the suggestion by Payne (1968) that sheep may be a late Pleistocene or early Recent derivative of goats. Our interpretation is, instead, that the evolution of the functional complex of male agonistic behavior and cranial morphology, so fundamentally different in goats and sheep, has been progressing for several million years. The necessity for postulating a relatively long period of gradual evolutionary change is supported by Pilgrim's (1947) statement that fossil sheep have been recovered from the upper Pliocene and by the evidence summarized by Kurtén (1968) that *Capra*, *Hemitragus*, and *Ovis* have all been present in Europe at least

for much of the Pleistocene. We do not, in addition, find convincing Payne's suggestion that all living Caprini form a coenospecies, with potential gene-flow possible throughout all populations of the tribe. On the other hand, we are hopeful that the evidence presented in this paper on the correlation between male behavior and cephalic morphology in different Caprini will provide paleontologists with insights into the behavior of populations of Caprini represented by fossils.

The evolution of Caprini has been distinguished by the evolution of the ability to live safely in mountainous areas by virtue of large size and increased agility. These factors, we feel, have contributed to the convex survivorship curves that appear to distinguish the larger species. Increased survivorship, we have pointed out, in concert with a curved horn that permits non-mortal combat, makes adaptive the growth of larger horns and the evolution of delayed reproductive patterns among males.

ADDENDUM

While the present article was in page proof, a fine book on sheep by Geist (1971) appeared, clarifying several factors of behavior, particularly of Bighorn and Stone's sheep in western Canada. He emphasizes that larger-horned males are dominant to smaller-horned, that the most intensive combat ("jousting") is between strange males with horns of equal size, that the winner gains dominance, and that the more dominant males (invariably those younger adults with the largest horns) irregardless of age are relatively more successful in the rut and thus sire the majority of the next year's lambs. Thus selection against small-horned rams is intensive, but selection *for* all of the characters of head and horn whereby jousting rams resist concussion is also intense, as we had concluded before seeing Geist's book.

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PLATES



PLATE I. ♂ *Nesotragus moschatus*, a primitive bovid skull.



PLATE II. ♂ *Rupicapra rupicapra*, sectioned horn core showing only slight penetration by the frontal sinus.



PLATE III. ♂ *Nemorhaedus goral*, a generalized rupicaprine.



PLATE IV. ♂ *Capra hircus aegagrus*, skull with horn sheaths showing damage due to fighting.



PLATE V. ♂*Capra hircus aegagrus*, skull with horn sheaths removed.



PLATE VI. ♂ *Capra ibex sibirica*, young



PLATE VII. ♂ *Capra ibex sibirica*, young, with horn sheaths removed.



PLATE VIII. ♂*Capra ibex nubiana*, frontlet and horns of adult.



PLATE IX. ♂ *Capra ibex sibirica*; parasagittal section of skull, showing frontal sinus and septa, position of base of horn, and primitive configuration of skull. (In this specimen, the right horn was abnormal, having grown in a tight spiral.)



PLATE X. ♂ *Hemitragus jemlahicus*, adult.



PLATE XI. ♂ *Hemitragus hylocrius*, adult.



PLATE XII. ♂ *Hemitragus hylocrius*, adult, skull with horn sheaths removed.



PLATE XIII. ♂ *Ammotragus lervia*, adult.

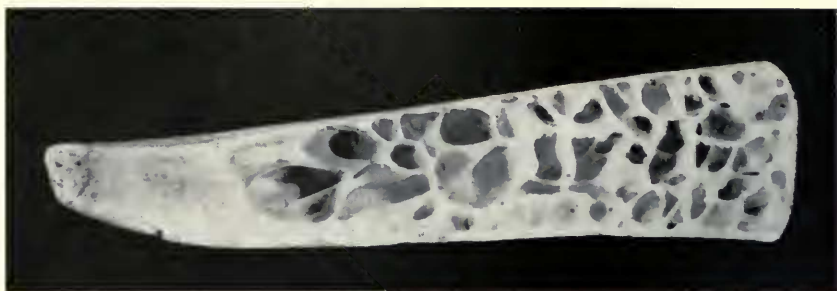


PLATE XIV. ♂ *Ammotragus lervia*, longitudinal section of horn core in frontal plane.



PLATE XV. ♀ *Ammotragus lervia*, adult.



PLATE XVI. ♀ *Ammotragus lervia*, skull with horn sheaths removed.



PLATE XVII. ♂ *Pseudois nayaur*, adult, showing areas of injury to the horns.



PLATE XVIII. ♂ *Pseudois nayaur*, skull with horn sheaths removed.



PLATE XXI. ♂ *Orvis musimon*, adult.



PLATE XXII. ♂ *Ovis canadensis*, 5+ years.



PLATE XXIII. ♀ *Ovis canadensis*, adult.



PLATE XXI. ♂ *Oris musimon*, adult.



PLATE XXII. ♂ *Ovis canadensis*, 5+ years.



PLATE XXIII. ♀ *Ovis canadensis*, adult.



PLATE XXIV. ♂ *Ovis canadensis*, adolescent, with frontal surface of horn core removed.



PLATE XXV. ♂ *Orvis canadensis*, horn core sectioned longitudinally.



PLATE XXVI. ♂ *Ovis canadensis*, para-sagittal section through skull.



PLATE XXVII. ♂ *Ovis canadensis*, horizontal section through the left frontal sinus and left horn core. Frontal bone and frontal surface of core have been removed.

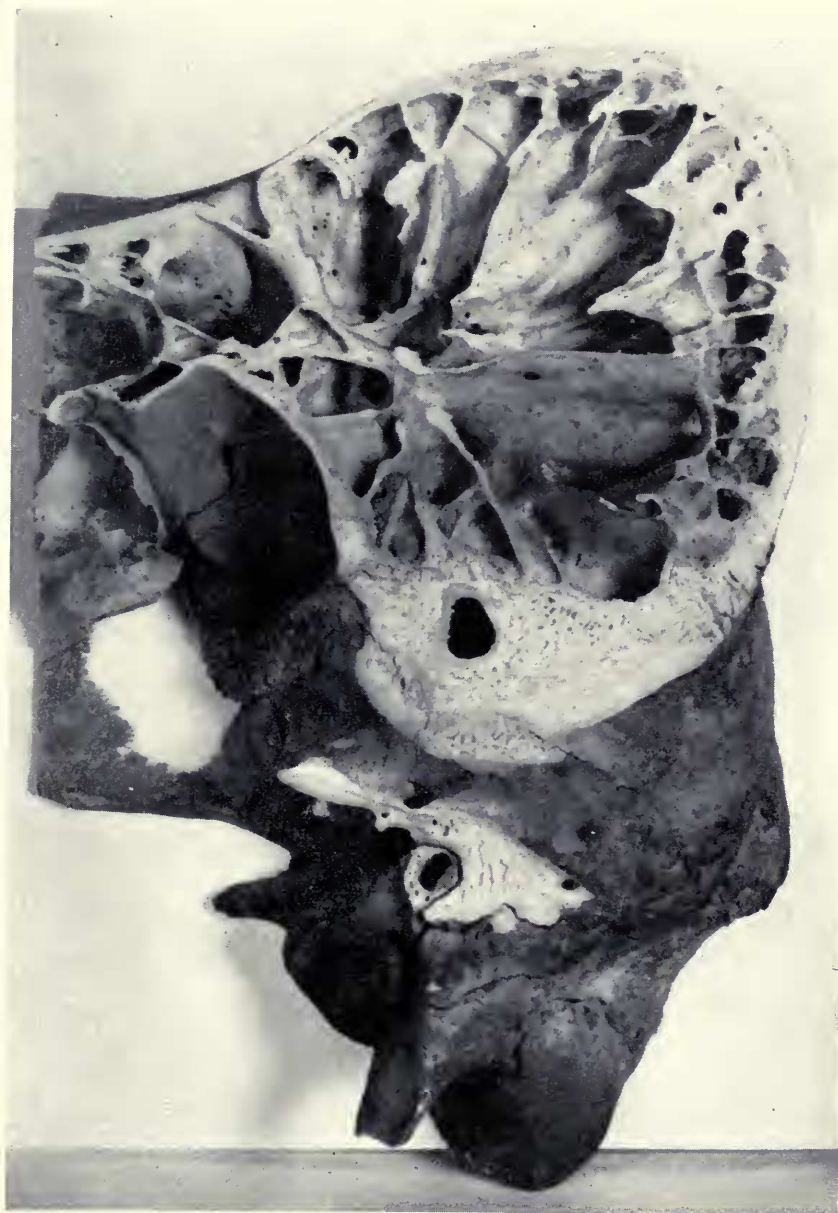


PLATE XXVIII. ♂ *Ovis canadensis*, cross-section at base of horn core.



PLATE XXIX. ♂ *Oris ammon*, skull with horn sheaths removed.



PLATE XXX. ♂ *Oris ammon*, para-sagittal section of skull.



PLATE XXXI. ♂*Ovis ammon*, horn core with longitudinal section through base.



PLATE XXXII. ♂*Ovis musimon*, transverse sections of horn, including sheath, from base (top left) to more distal (bottom right).



PLATE XXXIII. Transverse sections of caprine horn cores: Top (left to right): *Ovis ammon* ♂, *O. canadensis* ♂, *O. musimon* ♂; Bottom (left to right): *Ammotragus lervia* ♂, *A. lervia* ♀, *Capra hircus aegagrus* ♂.

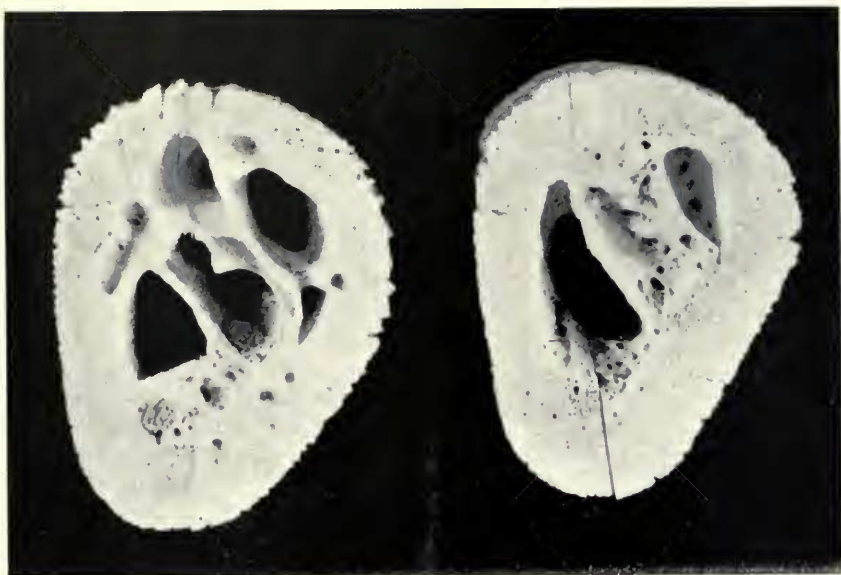


PLATE XXXIV. ♂*Oris ammon*; transverse sections of horn core; proximal section is at left, more distal at right.